Pollen studies in semi-arid areas : North East Iran and South West Spain.

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POLLEN STUDIES IN SEMI-ARID AREAS:

NORTH EAST IRAN AND SOUTH WEST SPAIN

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ABSTRACT

Fossil and modern pollen studies have been conducted in N.E. Iran and S.W. Spain, from which models of modern pollen movement in desert and mediterranean communities are proposed and compared. The modern pollen data was also used to aid interpretation of the fossil pollen diagrams from N.E. Iran and S.W. Spain. It was possible to differentiate in S.W. Spain many of the major mediterranean plant communities on the basis of their associated modern pollen rain, this however, was not possible in N.E. Iran. The fossil pollen diagrams from N.E. Iran revealed a relatively stable vegetational history, with possibly changes in the forest composition of the Caspian forests being reflected in changes in the long distance input to the fossil site. The diagrams from S.W. Spain, exhibit however, marked changes in the forest composition of the Doñana area. The earliest diagrams dated to approximately 13,000 b.p. reveal the existence of a local sand dune succession, the long distance component of which reveals the possible presence of a cool moist forest on the Guadalquivir plain at this time. The next fossil site is dated to approximately 4550 b.p. and reveals the presence of a mediterranean forest already heavily disturbed (possibly due to tectonic activity) which recovers only to be disturbed once again. This second disturbance may be due to an anthropogenic effect since large amounts of Vitis pollen are recovered from this time. Subsequently the viticulture is abandoned around the time of the Romans and the forest recovers only to be heavily disturbed once again as the Moorish influence acts on the vegetation. (The three main components of the forest vegetation are found to exhibit very different behaviour during the disturbances). The third site reveals the nature of the vegetation from

1740's onwards when the site was thought to have last been disturbed by sand dune activity. The core reveals the existence of scattered Pinus in monte negro vegetation from which the Pinus is subsequently progressively removed. The final stages of the diagram reveal the invasion of the site by Quercus suber and its subsequent dominance in the community.

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PART A

POLLEN STUDIES IN N.E. IRAN

CHAPTER 1

Introduction

Iran is a vast country of some 1.5 million km^2, and the land varies from below sea level on the Caspian coast to 5770m on Mount Damavand. Most of the land is above 1200m, and there is a great contrast in vegetation types between the humid forests of the Caspian to the semi-arid areas of Central Iran. The temperature can vary between $-35^{o}C$ in winter in the North West to $50^{o}C$ in summer in the Persian Gulf.

Geologically Iran occupies part of the Tethyan geosynclinal belt, which extends from Morocco to Indonesia. The Iranian sector was compressed between the Russian platform and the Arabian shield, the Elburz and Zagros mountains being the result of this compression.

The pollen study was situated in an area of North East Iran, known as the Turan. In this area, a multidisciplinary research programme (Turan programme) attempting to combat and monitor desertification has been based. The Turan programme was set up in response to a United Nations call to study desertification, with the aims of establishing baselines of information on the interactions of human activities and natural processes in a range of different sites that are vulnerable to desertification. However, due to events beyond our control in Iran this project has now been terminated. The results of the pollen study conducted so far, are discussed in chapters 2 and 3.

The Turan Biosphere Reserve (so designated as part of the Man

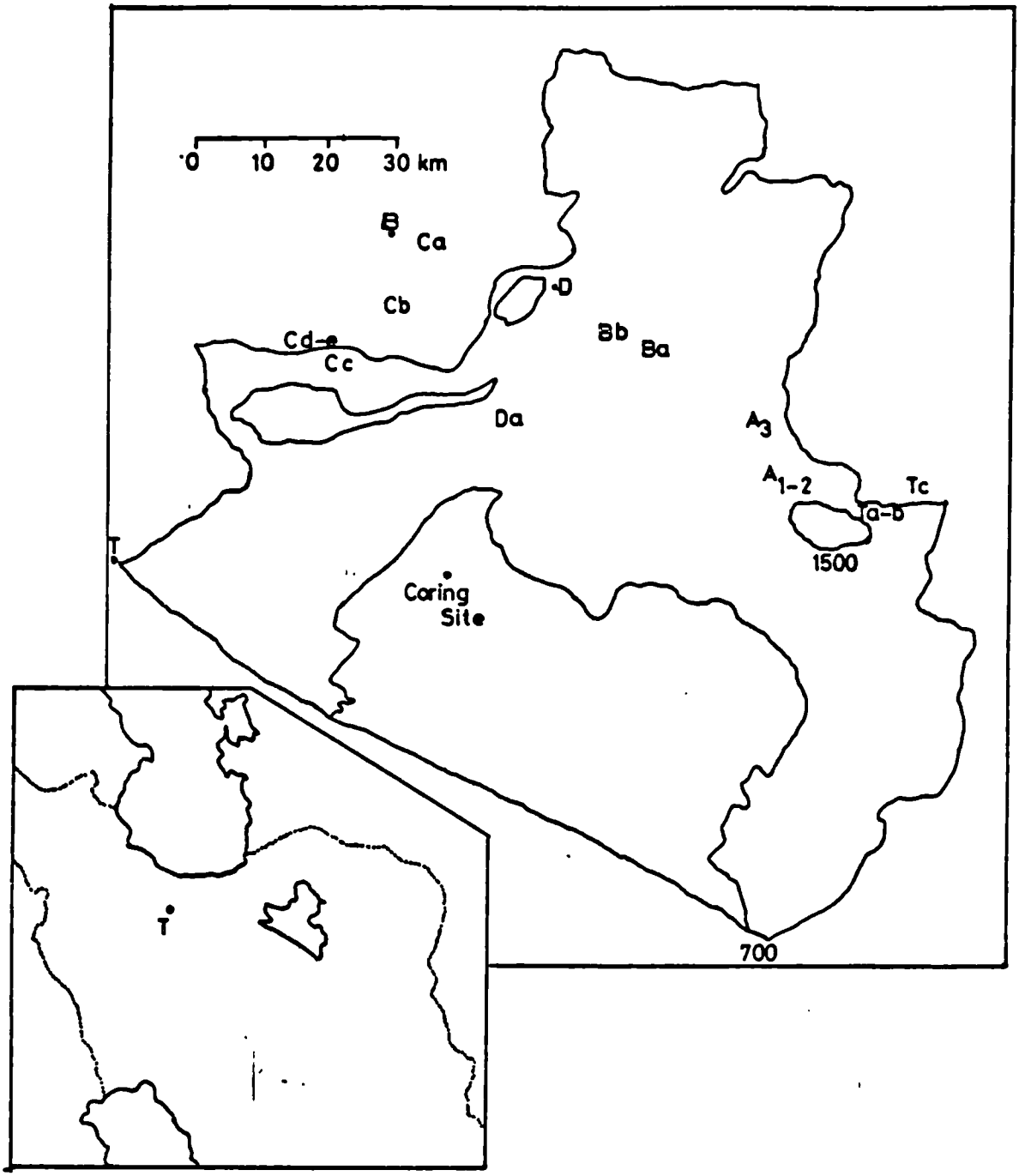


Fig. 1. Map of the Turan study area, including position of coring site and surface samples.

TURAN BIOSPHERE RESERVE

Preliminary Vegetation Map

Fig.2

- Primary Roads
- Secondary Roads
- Contour Lines (in meters)
- *Rivers*
- Intermittent Rivers
- Turan Biosphere Reserve Boundary
- Turan Wildlife Refuge Boundary
- Area of Map 4 (KHAR & TAURAN)
- Area of Map 3 (CENTRAL TAURAN)
- Sand
- *Kavir*
- Mountains (elevation in meters)
- Villages
- Ruins
- Summer Sheep Stations
- Sheep Pens

Chah - Well
Kal - River Channel
Kalata - Minor Settlement
Kavir - Playa
Kuh - Mountain
Qala - Fort
Qolla - Mountain Peak
Shoqa - Playa
Shur - Saline

HALOSOLA - SYSOPHYLLUM COMMUNITIES

- Variant of *Halocylon aphyllum*
- Dominated by *Sysophyllum eurypterum*
- Dominated by *Salsola tomentosa*
- Variant of *Aellenia glauca*
- Variant of *Ganaanthus gamocarpus*
- Variant of *Cousinia turkmanorum*

ARTEMESIA SPP. *HERBA-ALBA - EPHEDRA INTERMEDIA - AMYGDALOS CF. LYCIOIDES* COMMUNITIES

- *Amygdalus lycioides - Atraphaxis spinosa* communities
- *Amygdalus - Hypocylix* communities
- *Amygdalus - Hypocylix* communities in complex with *Salsola - Sysophyllum*
- Variant of *Cousinia cf. neurocentra*
- Variant of *Ganaanthus gamocarpus*
- Variant of *Cerasoides latana*

ASTRAGALUS STROBILIFERUS - COUSINIA MESHEDENSIS COMMUNITIES

- *Astragalus strobiliferus - Amygdalus* communities

STIPAGROSTIS - CALLIGONUM COMMUNITIES

- *Stipagrostis pennata - Calligonum* communities
- *Stipagrostis karelinii - Zeirnovia* communities

- BARREN KAVIR
- Dense Annual Halophilous Vegetation
- Shrubby Salt Marsh Communities

KHAR

TAURAN

UNIVERSITY CARTOGRAPHICS - HENRY WRIGHT / JOHN BEE

MAP 2

and Biosphere programme of U.N.E.S.C.O.) covers a surface area of 18,420 km^2 with a circumference of 665 km (see Fig.1) and is situated at the North East extremity of the Great Salt Desert (Dasht-e-Kavir) of the Central Iranian Plateau. It occupies a position $34^{o}45'$-$36^{o}30'$ latitude north and 55^{o}-57^{o} longitude east. The reserve includes the province of Sharud and part of the province of Khoranshan, and is separated from the Caspian by the Elburz range of mountains, which acts as a major factor in preventing moisture laden winds from reaching the Kavir basin.

The reserve presents a variety of habitats, including three extensive plains at different altitudes varying from 700m-1400m, a saline river system, three mountain systems rising to a maximum of 200m, large areas of steppe, some 200,000 hectares of sand, including mobile sand dunes, and an expanse of salt desert (Kavir). The 200m isohyet is considered to pass through the northern part of the area and the southern plain receives less than 100mm average rainfall per year (though no meteorological stations are maintained in the area). A light snow covering occurs on the higher northern plains for short periods. The central salt river flows only intermittently throughout the year. Rainfall of several millimetres at a time generates sheet run off and wadi flooding; it occurs mainly in the winter with none during summer. Springs occur at the base of the mountains and soils are generally sandy except for the Kavir which is solonchak.

Vegetation varies according to land form and secondarily responds to human influences. A preliminary vegetation map

based on the work of Freitag is included (Fig.2). Surrounding the Kavir is a thin belt of shrubby saline communities dominated by Haloxylon persicum followed by a belt dominated by Zygophyllum eurypterum and Salsola sp. with occasional variations such as Haloxylon and Aellinia. At higher elevations an Artemisia steppe predominates with species such as Amygdalus lycioides and Ephedra intermedia. Higher still on the limestone outcrops, above the 1500m contour, an Amygdalus/Atraphaxis community dominates. The highest points are dominated by an Astragalus strobiliferus/Cousinia community sometimes again with Amygdalus. The central salt river carries a saline type of vegetation. Perennial cover varies from 5-40%. For a detailed vegetation see Freitag (1982) and for a preliminary species list see (Rechinger 1977).

The predominant human activity is pastoralism (Spooner 1980) of various types, both sedentary and transhumant. Some 150,000 goats and sheep winter in the area from November to May, of which 25,000 belong to the local settled populations, who remain in the area during the summer. The local population also keep camels, donkeys and a few cattle. Agriculture is also important around most villages and is conducted by irrigation from qanats (Horne 1980), diversion of run off (Evenari 1971) and to a limited extent dry farming. The total human population of the area is approximately 3000,

The impact of the local population on the vegetation is quite marked. The woody shrubs, e.g. Zygophyllum, Artemisia and Haloxylon, are collected extensively for firewood and this has lead to overexploitation of the areas around

villages, leaving them barren except for annuals and plants that hold a religious significance or are unpalatable, an example of this being Peganum harmala. Overgrazing by sheep and goats also exacerbates this problem.

The geology of the Great Kavir and Great Kavir watershed have been discussed in detail by both Bobek (1959) and Krinsley (1970). It is generally thought that the Kavir has evolved under generally arid but periodically more humid climatic conditions. A brief geological history of the Kavir area now follows.

The Central Iranian Basin was invaded by a shallow sea through gaps in the embryonic Zagros mountains during early Oligocene times. At the beginning of the Miocene, the depositional environment changed from marine to brackish and eventually to lacustrine-terrestial. Brackish deposits alternated with terrestial deposits as sedimentation kept pace with subsidence of the basin. These deposits are known as The Upper Red Formation. The Central Iranian Basin was closed off from the sea in Late Miocene times.

Pliocene conglomerates overlie the Miocene deposits unconformably and represent gravel fans which spread out along the peripheral mountain fronts during a period of mid-Pliocene uplift. In the late Pliocene a strong regional diastrophism occurred which warped both Miocene and Pliocene deposits into their present anticlines, dunes and minor basins, which contribute to the structure of the Kavir. The anticlines and dunes of the Kavir have all suffered

denudation and most of the resulting material has been deposited in the Kavir basins.

Both Bobek and Krinsley have observed a recent rise in ground water and this is thought to represent a move to a more humid climate. The Kavir at one time was considered to represent a dried out and filled up lake (Hedin 1910) and (Gabriel 1957). However, it is clear that the reported beachlines or terraces can be explained as erosion features due to recent tectonism or to the structure of the Miocene deposits at the surface (Krinsley 1970). There is no unequivocal evidence that a lake ever covered the entire area of the Kavir.

No pollen work has previously been conducted in North East Iran, but several studies have been carried out in North West Iran, such as those of Van Zeist and Bottema (1977), and Wright, McAndrews and Van Zeist (1967) and by Van Zeist, Woldring and Stapert (1975) in S.W. Turkey and Van Zeist, Timmers and Bottema (1968) in S.E. Turkey.

CHAPTER 2

CURRENT POLLEN RAIN STUDIES IN TURAN

As has been mentioned in the previous chapter, a thorough study of the current pollen rain in any desert area is a valuable aid to palaeoecological interpretation of fossil pollen profiles. Therefore, for the purposes of a pollen survey, five vegetation types were selected. Plant nomenclature follows K.H. Rechinger (1963) Flora Iranica. All samples were collected by Moore (1977).

(i) Limestone outcrops. Isolated hills in the area rise to heights of 2280m and are separated by alluvial plains. Upon these hills, scattered trees of Pistacia khinjuk grow, and there is an abundance of the shrub Amygdalus lycioides. Three sites were examined from this zone - Ta, A1, A2.

(ii) Ephedra zone. Around the base of the rocky hills there is often found a band of vegetation in which Ephedra is found. Two species E. strobilacea and E. intermedia occur in the area, but the latter is more frequent in this zone. Two sites were examined Tc, Da.

(iii) Zygophyllum-Artemisia zone. Extensive areas of the alluvial plains are dominated by the shrub Zygophyllum eurypterum, with smaller bushes of Artemisia herba-alba growing amongst it. Six sites were studied Ba, Bb, Ca, Cb, Cc, A3.

(iv) Saline areas. In the vicinity of the Kal-e-Shur salt river, around the edge of some undrained basins and especially around the edges of the Kavir, there exist areas with saline soils. These are dominated by Chenopodiaceae (Zohary 1973). Two sites are described Ce, Cd.

(v) Disturbed areas. Near human settlements, whether temporary as in the case of sheep pens, or permanent as in the case of villages, a considerable degree of vegetation disturbance has often ensued as a result of grazing pressure and fuelwood gathering. Vegetation consists of either annual species or unpalatable herbaceous perennials, particularly Peganum harmala.. One site was examined, Tb.

Method of Sampling

The sites examined were chosen subjectively as representative of the vegetation type. Wherever possible the sample area was located in the centre of an extensive stand of uniform vegetation. An area 10m by 10m was marked out and all the shrubs and perennial herbs were counted. Since sampling took place in March, when some perennial geophyte and hemicryptophyte species had not commenced growth, it is possible that some species were overlooked. Other species present in the square were listed; these often included many annual species that were growing abundantly at the time of sampling. Other species found in the vicinity, but not within the sample quadrat were listed separately. It was not always

possible to identify every species.

From within the square, ten samples of surface sand with its content of organic debris were collected, each sample being of about $5cm^3$ in volume.. These were mixed together thoroughly and transported and stored in polythene containers at low temperatures (2^oC). A single subsample of about $1cm^3$ was eventually used for pollen analysis.

Adam and Mehringer (1975) have discussed the use of various sampling methods in their surface studies of the desert grasslands of Arizona. They found a considerable variation in pollen content of surface deposits even when collected close together and in winter (when local over-representation of flowering species would not be a problem). They found at least five samples were necessary to provide a representative mean value for the major constituents of the pollen spectrum. For this reason it was considered that a mixing of ten such samples, followed by subsampling, would provide an adequate representation of the local pollen rain.

Preparation of the samples was as given in Appendix B but with an extended HF phase of three hours. The pollen was stained with safranin and mounted in glycerol jelly. Approximately 500 pollen grains were counted for each sample and identifications made using type material from the area, and from material collected from Ariamehr herbarium, Tehran.

The precise locations of the sites sampled are shown in Fig.1. Detailed vegetation descriptions are given in Table 1 and Fig. 3 and 4). Some comments on the identification of pollen

TABLE 1

VEGETATION ANALYSIS OF SURFACE SAMPLE PLOTS

	A1	A2	A3	Ba	Bb	Ca	Cb	Cc	Cd	Ce	Da	Ta	Tb	Tc
Anacardiaceae														
Pistacia khinjuk	0	1										-		
Caryophyllaceae														
Acanthophyllum diezianum	1											1		
Chenopodiaceae														
Halocnemum sp.								+						
Haloxylon persicum				4				+	21	20				
Salsola spp.			6					1						
Unidentified spp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Compositae														
Artemisia herba-alba	28	3	5		2	123	53	45	22	1	16	9	0	
Centaurea spp.												2		
Crepis sp.													+	
Echinops sp.						1								
Lactuca sp.	1											9	+	
Cruciferae														
Alyssum sp.	+						+		+			+	+	
Unidentified spp.						+							+	
Cyperaceae														
Carex sp.														+
Ephedraceae														
Ephedra intermedia											3			31
Geraniaceae														
Erodium sp.		1												
Gramineae														
Bromus sp.	+						+		++		+	+	+	+
Poa bulbosa													+	
Stipagrostis sp.			0											
Leguminosae														
Astragalus sp.														2
Liliaceae														
Gagea recticulata	0	2												
Polygonaceae														
Calligonum sp.			2											
Pteropyrum aucheri			2											
Primulaceae														
Androsace maxima		+												+

	A1	A2	A3	Ba	Bb	Ca	Cb	Cc	Cd	Ce	Da	Ta	Tb	Tc
Ranunculaceae														
Anemone biflora	0											+		
Ceratocephalus falcatus	+				0		+		+				+	
Thalictrum isopyroides	39													
Rosaceae														
Amygdalus lycioides	4	2										12	0	
Scrophulariaceae														
Scrophularia striata												3		
Veronica spp.	+												+	
Tamaricaceae														
Tamarix sp.			0											
Valerianaceae														
Valerianella sp.													+	
Zygophyllaceae														
Peganum harmala			5		0	2						0	31	
Zyogphyllum eurypterum	1		1	1	3	1	2	2			2	0		

All numbers refer to densities of the species per 10m x 10m quadrat.

+ = Species present in the quadrat, but density could not be readily estimated.

0 = Species not present in the quadrat, but present within 10m of the quadrat.

Table 2

Pollen analyses of surface samples (see also Figs. 2 and 3)

	Ta	Tb	Tc	Td	Aa	A_2	A_3	Ba	Bb	Ca	Cb	Cc	Cd
Trees													
Acer						0.2							
Alnus	0.4	0.2	0.8		0.2	0.2		0.4	0.6	0.6	0.2	0.4	1.0
Betula			0.4		0.2								
Carpinus	0.2	0.7	0.6			1.2	0.8	0.6		0.4	0.8	1.2	0.6
Cedrus						0.4							
Corylus					0.2	0.2				0.2			
Fagus						0.2				0.2			
Fraxinus			0.2										
Juglans		0.4										0.4	0.6
Juniperus					0.4				0.2				0.6
Pinus		0.2							0.2			0.2	
Pistacia	0.2		0.6								2.0		
Platanus		1.1	0.4										
Populus						0.4							
Pterocarya	0.2	0.4			0.2				0.6				0.2
Quercus			0.2			2.6	0.6	1.4		0.2	0.2		0.6
Shrubs and Herbs													
Acantholimon type	0.2		0.4							0.6	0.2		
Acanthophyllum type	0.2	0.9			0.2								
Alhagi type									0.2				
Amygdalus type	0.2				1.2								
Anemone type	1.6				2.4						0.2		0.2
Aster type					0.2								
Astragalus type					0.2				0.2				
Atraphaxis			0.8			0.2			0.4				
Bidens type		0.2	0.6		0.4		0.2	0.4				0.4	
Boraginaceae					0.8				0.2				
Buplurum type							0.2						
Caccinea type			3.2										
Caryophyllaceae								0.8		0.8			
Centaurea	0.2						0.2						
Cerastium type					0.2	0.6		4.0					
Ceratocephalus type	0.2	1.3			0.6								
Consolida type					0.6								
Cousinia type	0.6	0.4				0.2							
Cyperaceae		3.3	0.4		0.2	0.4			1.0			0.2	0.6
Ferula type									0.6				
Jurinea type			0.2		0.2								
Labiatae					0.2				0.6		0.6		0.6
Leguminosae	0.2		0.6		0.4						0.4		0.2
Liliaceae		0.2			0.2				0.8				
Nepeta type													
Plantago lanceolata		0.6		0.4									
P. major type	0.2												
Polygonum	0.4												0.2
Potentilla type			0.2										
Prangos type	0.2				0.2				0.2		0.2		0.2
Psammogeton type								0.2	2.0			0.8	2.0
Pteridium										0.2			
Pteropyrum			0.2										

	Ta	Tb	Tc	Td	Aa	A_2	A_3	Ba	Bb	Ca	Cb	Cc	Cd	C
Rosaceae (undiff.)						0.2								
Ranunculus acris type			0.2											C
Rheum			0.2		1.4									C
Rumex (undiff.)		0.2												C
Rubiaceae		0.2												
Salsola type												23.2		
Scabiosa		0.2												
Scrophularia type		15.4			0.2				0.2					
Sparganium type			0.2											
Spergula type							0.2							
Tamarix									0.2					
Thalictrum	1.2	0.6	0.4		6.4	1.6	1.2	0.2		0.6			0.2	
Tribulus type						0.2								
Umbelliferae (undiff.)								0.4						
Veronica type					2.0						0.2		0.2	
Zosima type						1.0	1.2	0.4		0.2		0.8		

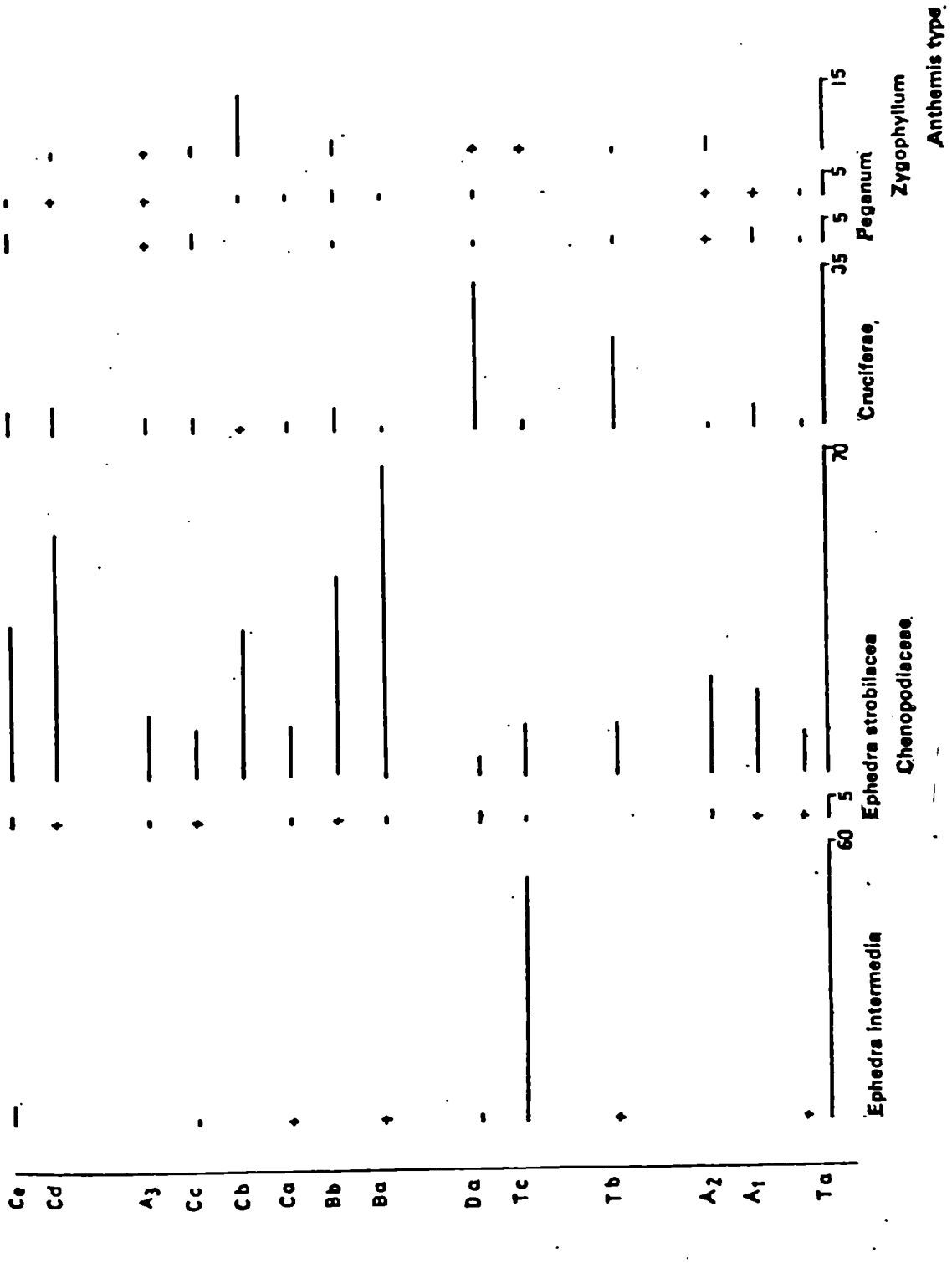


Fig.3. Selected surface sample results

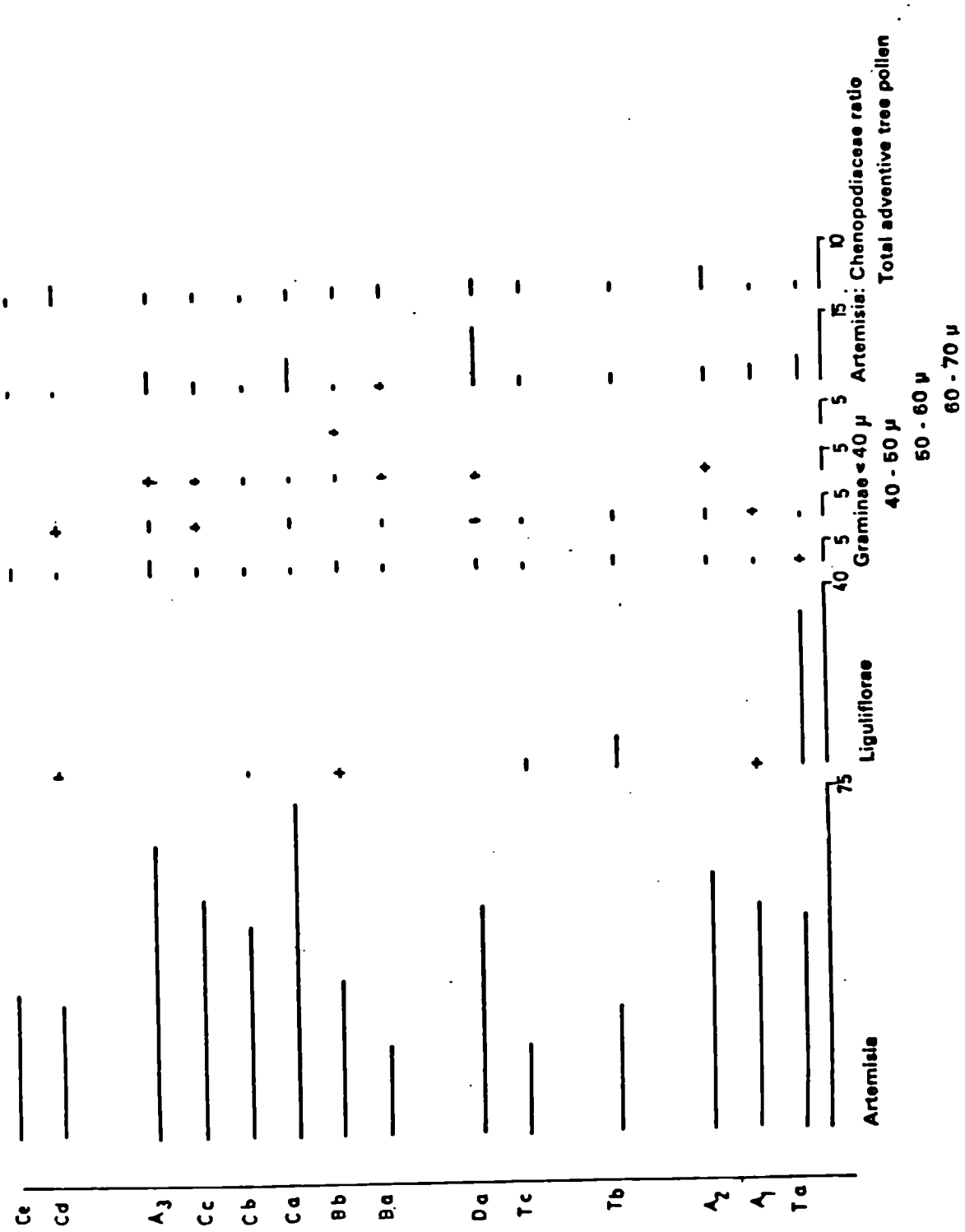


Fig. 4. Selected surface sample results

grains are located in Appendix A. Seven sites were counted by Dr. P.D. Moore and are included to provide a complete picture of the local pollen rain of the Kavir area.

Discussion of the Pollen results

The most obvious feature of the pollen data is the high representation of Artemisia and the Chenopodiaceae in all the samples. This is in accordance with the findings of Wright, McAndrews and Van Zeist (1967) in their analysis of surface samples from Artemisia steppe in West Iran. They had nine samples from near Tabriz and these possessed an average Artemisia representation of about 25% and a chenopod representation of about 45%. This feature of the pollen rain from Artemisia steppe was also found by Bottema and Barkoudah (1979) in their study of sites from Syria and Lebanon, but they also found large amounts of Plantago pollen in the pollen rain, which is a feature not found in the Turan study. Wright et al (1967) in North West Iran also found low amounts of Plantago in samples from Artemisia steppe but found higher values in samples taken from a Mesopotamian steppe near the Mediterranean. Other samples have been taken from steppe floras in South West Turkey by Van Zeist et al (1975) and in South East Turkey by Van Zeist et al (1968). The results from S.E. Turkey have low levels of both Artemisia and chenopods. This is probably due to the absence of Artemisia herba-alba from the steppe flora of S.E. Turkey and that the saline habitats in which chenopods tend to thrive are rare in that area. The one sample taken from an Artemisia fragans steppe in S.W. Turkey had a 34% of

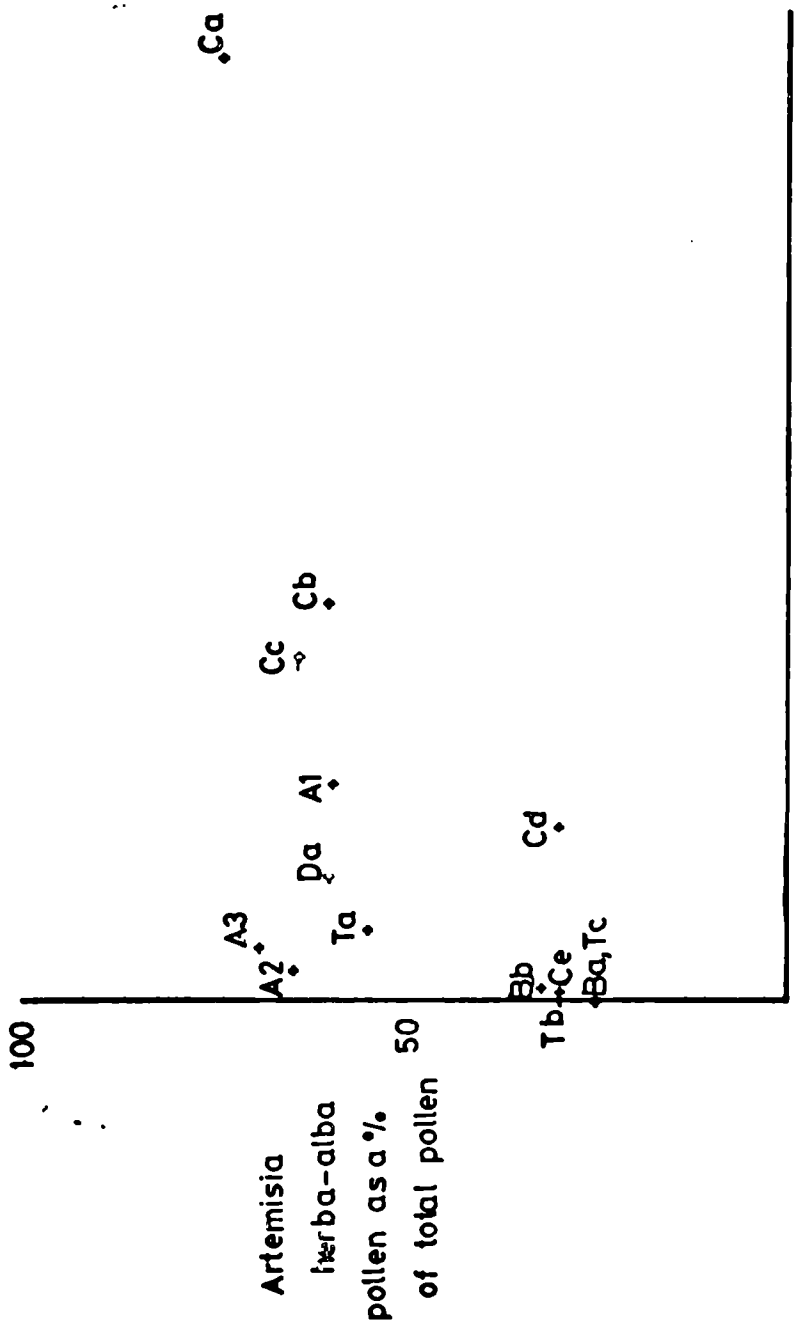


Fig.5. Relationship between density of Artemisia herba-alba plants and amount of pollen recovered from surface samples.

Artemisia pollen rain which again is in agreement with the results obtained in the Turan study. Fig. 5 represents a scatter diagram of the percentage of Artemisia pollen correlated with the number of Artemisia herba-alba plants in the various sites. One interesting feature about the pollen rain of Artemisia herba-alba is that even when no Artemisia plants are found in the immediate vicinity, e.g. sites Ba and Tc the pollen rain of Artemisia still reaches 25% and thus exhibits good dispersal. It also seems with two plants of Artemisia present in the quadrat the percentage of Artemisia in the pollen rain can be as high as approximately 60%. There is little fluctuation from this figure as numbers of plants increase except for site Cd where the high pollen percentages of the chenopods may have depressed this value. Once the values have reached 60% it seems to stay relatively constant until 50 plants are present and then even a doubling of the Artemisia population leads to an increase in its pollen rain of only 15%. Thus the Artemisia values are fairly insensitive to large variations in the number of Artemisia plants present. This effect will be of importance in the interpretation of a decline in the Artemisia totals which is seen in the fossil pollen spectrum from the Great Kavir, which is discussed further in a later section. It thus seems that Artemisia will be over-represented in at least a proportion of sites examined, i.e. in sites with only two plants present it will be over-represented but this may not hold true for sites where 100 or more plants exist. Over-representation is a common feature of wind pollinated plants, though it will be seen that this does not always hold true of Pistacia. Of course, the values of

Artemisia will also depend on the pollen productivity of other plants in the area being sampled and also on the pollen sum used in subsequent analysis.

Little can be said about the Chenopodiaceae due to the presence of unquantified numbers of unidentified annuals belonging to the Chenopodiaceae. Though it seems that they may exhibit the same characteristic shown in Artemisia, since four plants of Haloxylon persicum in site Ba give a 70% pollen representation in the pollen rain, while 21 plants in site Cd only give 60% representation in the pollen rain. So it appears that chenopod pollen proportions are not simply related to large changes in the chenopod population and thus will also tend to be over-represented in some of the sites analysed.

Insect pollinated plants, even when abundant, are poorly represented in the pollen rain, with the exception of certain types such as Cruciferae, Liguliflorae and Scrophulariaceae, which achieve high values in some sites, such as sites Da, Ta and Tb respectively. The cause of the high Cruciferae values in Da is unresolved though one of the unidentified plants may be the source of this pollen. The source of the high Liguliflorae is probably the nine plants of a Lactuca sp. noted in site Ta.

Under-representation, however, is particularly characteristic of certain shrub and hemi-cryptophyte species, even though they contribute most of the biomass. The main examples of shrubs are Amygdalus and Zygophyllum. Even though site Ta

Plate 1

Zygophyllum/Artemisia vegetation in the Kavir

Large bushes are Zygophyllum

Small bushes are Artemisia

had 12 plants of Amygdalus present, its pollen only reached 0.2%, the highest value coming from the four plants in site A1. This under-representation has also been found true in Western Iran by Wright et al (1967). Zygophyllum eurypterum is also under-represented; it is present in most of the sites and tends to be the dominant shrub present (Plate 1), but its pollen does not rise above the 2% in site Bb. It is interesting to note that Schoenwetter and Doerschlag (1971) found the same to be true of Larrea tridentata, which is also a member of the Zygophyllaceae, and is the dominant shrub in many semi-arid desert regions of the USA and Mexico. An example of a hemi-cryptophytic herb being under-represented is that of Peganum harmala. In site Tb its pollen representation only reached 1.0% when 31 plants were found; the highest values came from sites where no Peganum was observed to be growing. Thus it seems that most Peganum pollen production tends to be exported from the sites where it is produced. Again Peganum was found to be under-represented by Bottema and Barkoudah (1979) in their studies in Syria and Lebanon.

The pollen rain of Pistacia is of quite considerable interest for, since it is a wind pollinated plant, one would expect that its pollen would be well represented in the surface samples. But as one can see from the data, sites A1 and A2 that have the tree present in the locality do not have any Pistacia pollen, and elsewhere its pollen is found in only three out of the fourteen sites and does not go above 1%, (except in site Cb where it reaches 2.0%). This is quite a surprising result in the light of data from sites A1 and A2. However H. Freitag (personal communication) has noted clumps

of Pistacia in the hills to the south of this site which may provide the source of this pollen. This low representation of Pistacia was also found by Wright et al. (1967) in Western Iran where values only reached 4.5% when many trees were present. However, under-representation is probably a feature of the mode of reproduction (see pg.111).

The pollen of the shrub Ephedra is well represented in site Tc. Schoenwetter (1973) records 23% Ephedra from "short steppe" habitats at an altitude of 3900m in the Andes of South America. Welten (1957) obtained values as high as 72% in the European Alps, but found a rapid decline in the pollen type as he sampled at greater distances from the plants; similar data was obtained here, as at site Da. However, in Western Iran Wright et al. (1967), sampling at a site where Ephedra was common, found only 5% of its pollen and it was absent from most of the other sites. For a long time it was believed that Ephedra pollen was poorly dispersed, but the finding of grains over the Great Lakes of North America by Vinje and Vinje (1955) led Maher (1964) to question this assumption. It has since been found in small quantities in sites far distant from any source and is generally accepted as a pollen type capable of very long distance transport.

Gramineae pollen has been separated into various size classes, for cereal pollen grains are large (>40μ) and can sometimes be identified in this way; cereals are cultivated in the Turan villages. However, many grass genera produce large pollen grains (Beug 1961) and this is not, therefore, an entirely reliable means of segregation. Gramineae representation generally is very low, which reflects the paucity of

grasses in the Turan Biosphere Reserve which undoubtedly is maintained by the intensive grazing pressures. Levels of Gramineae pollen are lower than those found by Wright et al. (1967) in W. Iran and Bottema and Barkoudah (1979) in Syria and Lebanon, and are considerably lower than grass levels found in the Arizona desert by Schoenwetter (1971), where grass levels in the most xeric of habitats were about 15%.

For the rest of the herbaceous pollen types, they never seem to figure very highly in the pollen rain. This is in part due to their low pollen productivity and in part to high over-representation of Artemisia and Chenopodiaceae. An interesting point is that the grain of Sparganium type found must also represent long distance transport, since the genus is not recorded from the Central Iranian Plateau.

The tree genera present in the pollen rain present an interesting picture. In the area only Pistacia is growing naturally in the hills. Platanus orientalis, Populus sp. and Cupressus sp. are often planted around some of the villages. The rest of the genera, therefore, represent pollen transport from outside the area. The nearest area of deciduous forest is to be found on the north facing slopes of the Elburz mountains, about 300km to the North West of the study area (Zohary 1973, Sabeti 1976). The most frequent genus represented in all but two of the fourteen sites is Alnus, and which has been observed before to be part of a long distance component of pollen rain in deserts in the Sahara by Schulz (1980) and in Mexico by Schoenwetter (1974). Carpinus and Pterocarya are the next most frequent genera and neither of

these were found by Wright *et al.* (1967) in W. Iran. *Carpinus* and *Pterocarya* are restricted to the Elburz (Sabeti 1976), which suggests that the origin of the long distance Turan pollen is indeed the intervening Caspian forests. It is interesting to note that *Pterocarya* is capable of such long distance movement, for this type is frequently found in the fossil pollen flora of the Tertiary deposits of Western Europe (Machin 1971) and occasional grains of *Pterocarya* were found by Turner (1970) in Hoxnian interglacial deposits in Eastern England. However, the likelihood of long distance transport into these interglacial deposits is not high because of the local high pollen productivity of such environments that would lead to a dilution of the long distance component. A Caspian origin for the *Quercus* and *Pinus* pollen input can be postulated though these are not necessarily restricted to these forests. Again both of these types have been found to take part in long distance pollen rain from the studies in the Sahara and Arizona deserts and by Wright *et al.* (1967) in West Iran.

Fagus pollen probably derives from *F. orientalis*, the only Iranian member of the genus, which is also restricted to the Elburz mountains, as in the case of *Carpinus* and *Pterocarya* (Sabeti 1976). *Cedrus* is a genus not native to Iran, but is occasionally planted.

In Fig.2, total adventive tree pollen is shown as the percentage of the total pollen for all sites; values fall between 0.8% and 5% tree pollen. High values of tree pollen in unforested environments have also been found in tundra sites

by Lichti-Federovich and Ritchie (1968) and by Prentice (1980), and on oceanic islands such as the Shetland Islands, where Tyldsley (1973) was able to associate periods of tree pollen arrival with air mass movements from Scandanavia. McAndrew and Wright (1969), in the Great Plains of the USA, found Pinus pollen at 20% in the pollen rain, 300km from the nearest source. Singh et al. (1973) have also found values of Pinus of 5% 600km from the nearest source. Schulz (1980) has also found long distance arrival of pollen from Europe in Saharan sites, and Bottema and Barkoudah (1979) also record a similar picture in the unforested sites of their study in Syria and Lebanon.

It has been noted by many authors e.g. Birks (1973), that one of the main factors contributing to the high representation of long distance transported tree pollen in many tundra and desert sites, is the poor pollen productivity of the local vegetation. Long distance tree pollen records have reached 20% in studies by Lichti-Federovich and Ritchie (1968), Aario (1940 and 1944) in Lapland, Grichok (1950) in Russia, Terasmae (1967) in Western Canada and Prentice (1980) in Finnmark. However, this has not always been found to be true, e.g. the studies of Colinvaux (1964), Fresckild (1967), Iversen (1952). Hevly (1968), looking for regional pollen in surface samples from the Arizona desert, found no regional representation, just the high dominance of Compositae and Chenopodiaceae found in many semi-arid lands. Thus it may be that poor local pollen productivity will exaggerate the proportion of long distance pollen. This may be true of the Turan study, but absolute pollen influx values would have to

be obtained before this could be ascertained.

Also of great importance is the geography and aspect of the Area. It has been found that the prevalent wind direction at flowering times can also profoundly influence the proportion of long distance transported pollen in the samples. Since Ritchie (1974) found 30-40% AP in tundra sites in the Mackenzie area but in Manitoba (Lichti-Federovich and Ritchie 1968) in Western Canada the AP reached 40-60% of the total pollen. The predominance of Northwest, North and West winds from treeless regions or the ocean is thought to explain the depression of the long distance pollen in the Mackenzie results, while the predominance of Southerly blowing winds in the Manitoba region during the early summer is thought to increase the proportion of long distance transported pollen. In the Turan study the values of tree pollen input are low compared to these tundra sites. Thus it is possible that the poor local pollen productivity of the sites studied may only partly account for the values. Perhaps of greater importance are the factors of geography and aspect just mentioned, since the highest values in the Turan study were obtained from site A2, an exposed ridge in the eastern part of the reserve and at Cd, a low lying but westerly site. It is not known what the predominant wind direction is over the Central Iranian Plateau during spring but high winds have been recorded from the South West, P.D. Moore (personal communication). Such winds will have crossed many thousand kilometres of treeless vegetation before reaching Turan. Since the Caspian forests are situated to the North West of the study area, this may well explain the lower long distance

tree pollen input into the various sites compared to many other unforested environments.

When looking at pollen rain of treeless environments such as tundra and semi-arid sites, it must be borne in mind that the pollen transport models of Tauber (1965), which are applicable to temperate woodlands, have to be modified. Pollen transport in semi-arid environments involves three components (fig.6):-

(i) Long distance component that is comparable to Tauber's, but the importance of the component depends on a.local pollen productivity.
b.Prevalent wind direction at flowering time (Cl component of Tauber).

(ii) Canopy component direct onto the soil as in Tauber Cc.

(iii) Water component which comprises two different factors a. Rain out component of Tauber Cr.
b. Water fed movement of pollen at ground level in the form of sheet flooding etc. Csf.

This model differs from that of Tauber mainly because of the structure of the vegetation. The trunk-space component of Tauber, that can provide most of the pollen input into small basins is missing because of the low stature of the vegetation. However, another component does exist which can also provide most of the pollen input into basins and this is the Csf component. It will be seen in the case of the Kavir that the Csf component is by far the most important factor in providing

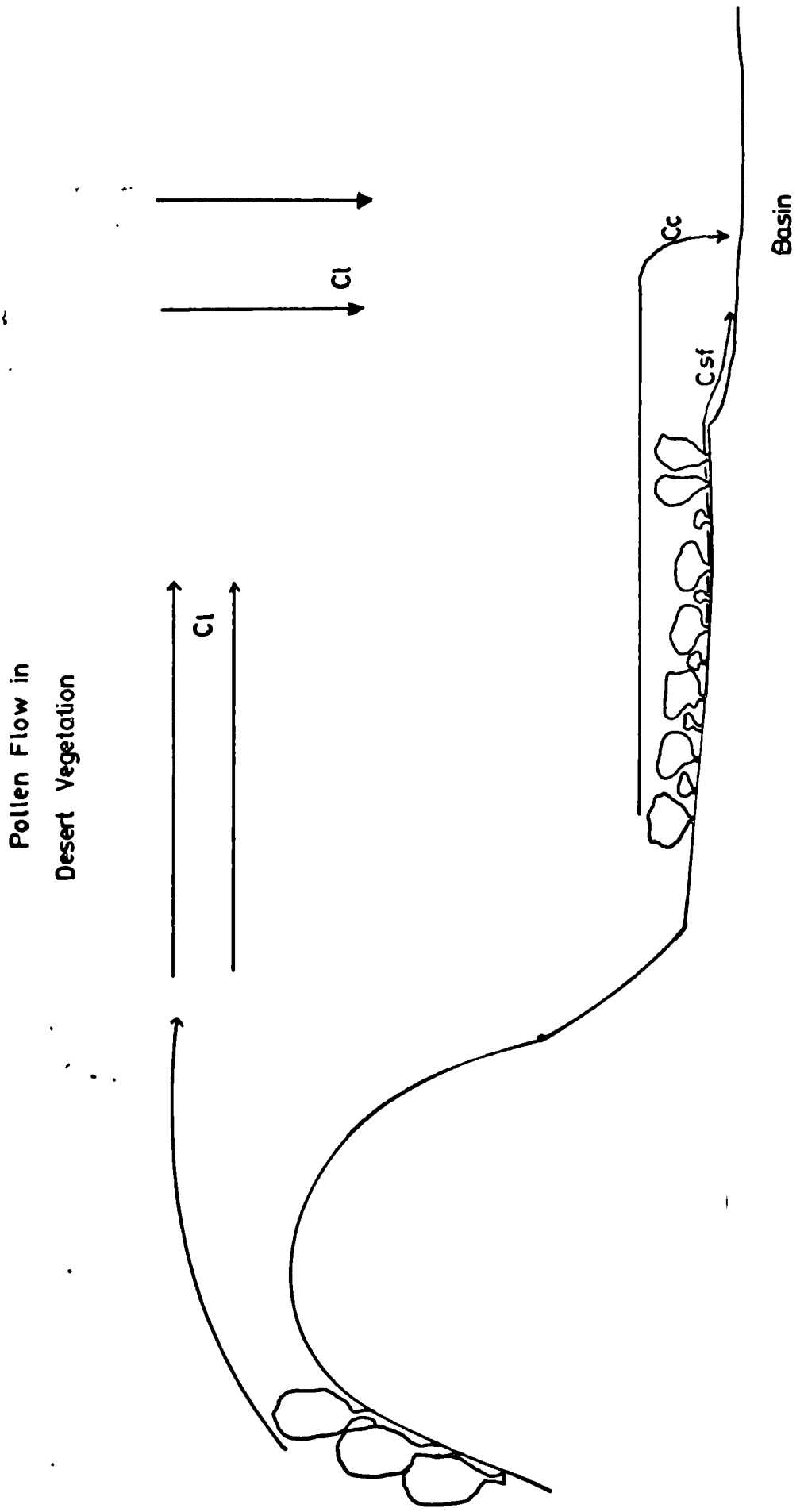


Fig.6

pollen input into the site.

So pollen input into many semi-arid sites such as this one will depend on the Cl, Cc, Cr, Csf components. The importance of each will vary according to the biological and geographical factors operating at each site. As has already been shown, the Cl component in many tundra sites and some desert sites can lead to the rest of the local vegetation being under-represented, but in the Turan study this component is of little importance compared to both the Cc and Csf components of the pollen rain.

One of the main aims of surface pollen studies is to permit the recognition of a plant community or vegetation type on the basis of its associated pollen rain. This, if it is possible, facilitates the process of interpretation in the examination of fossil pollen assemblages. From the limited number of surface samples which have been analysed from the Turan, it is evident that there is considerable variation in the pollen spectrum of sites from within the same vegetation type, e.g. Ta and Al or Ba and Ca. Also many of the most important species (in that they account for most of the biomass of the site), are not well represented in the pollen rain, e.g. Amygdalus, Peganum and Zygophyllum. Consequently, the separation of the communities on the basis of their pollen spectra is very difficult. One could look to 'indicator species' which show a certain degree of fidelity to certain communities, such as Thalictrum, Acanthophyllum and Ceratocephalus type, but the frequency of these taxa is too low, hence large sample counts and numerous replicates would be necessary to provide an adequate statistical basis for such

an interpretive technique.

The abundance of Chenopodiaceae and Artemisia pollen types has led to an examination of the possibility of using their ratio as a guide to the vegetation type. This type of work has been found of value in various other palaeoecological work. In North West Europe, the ratio of tree:non tree pollen has proved useful in studying prehistoric forest clearance, and Turner (1964) has developed an arable:pastoral index based on the ratio of the sum of various indicator species. Young and Schofield (1973) in analysing habitat changes on the Kerguelen islands, used the ratio of Azorella: Acaena. High values, they considered, represented a cool, upland climate, and low values a warm, lowland climate. Martin (1973) used the ratio of Myrtaceae:Chenopodiaceae in her studies of Quarternary changes in the vegetation of the Nullabar plain of South and Western Australia, high values being characteristic of mallee scrub and low values showed a dominance of the chenopods over the scrub vegetation. In their study of the pollen rain of N.W. India, Singh et al. (1973) were also able to use Artemisia and chenopods as indicators of aridity, with Artemisia becoming only really important when rainfall was about 500mm. But in the Turan Artemisia is dominant and the rainfall is considered to be only 200mm.

In the Turan studies the Artemisia:Chenopodiaceae ratio has been calculated for the fourteen surface samples analysed (Fig.3). The ratio is very variable within each of the vegetation types, especially within the Zygophyllum:Artemisia

zone and the Ephedra zone. The saline sites have strong, local contingents of chenopod species and produce very low ratios. Undoubtedly the picture is made difficult to interpret because of the ruderal members of the Chenopodiaceae which are present in many non-saline locations.

It may be possible to distinguish the effects of overgrazing and fuelwood gathering on the vegetation. Site Tb is a disturbed site but, although 31 plants of the grazing indicator Peganum harmala were present, very little of its pollen was picked up. In fact, more pollen was found where no Peganum plants were observed to be growing. There is also a slight tendency for an increase in Cyperaceae levels in disturbed soils. Again it has been observed that members of this family do tend to increase in response to grazing. However, a more complete range of samples is needed in order to try to separate mesic/xeric habitats and to distinguish the effects of overgrazing and fuelwood gathering.

CHAPTER 3

FOSSIL POLLEN IN THE TURAN BIOSPHERE RESERVE

A core was obtained from the north east corner of the Great Salt Desert Dasht-e-Kavir of the Central Iranian Plateau by Bhadresa and Moore in January, 1978. The position of the core is shown in Fig.1. The geomorphology of the Kavir has already been described in the introduction to the work. The sediments are sands and silts derived by fluviatile inwash from the surrounding slopes and hills during the spring melting of snows. Evaporation through the summer months leads to the deposition of gypsum layers in the sediments, which may become concreted..

A core of three metres in depth was obtained from a site approximately 1km into the Kavir beyond the last vegetation (Haloxylon persicum and other Chenopodiaceae). The core was obtained by a combination of excavation and the use of the Russian type corer (Jowsey 1966). It was transported by air and stored in rigid plastic tubes and kept in cold conditions ($2^{o}C$) in King's College, London, for approximately six months before analysis began. Samples were taken every 4cm. and pollen was concentrated using the techniques described in Appendix B. Approximately 500 pollen grains were counted at each level.

The concentration and the state of preservation of the pollen varied with depth; but was generally countable except between 210 and 270cm. The pollen diagram is shown in Figs. 7-9. All percentages are expressed as a percentage of the

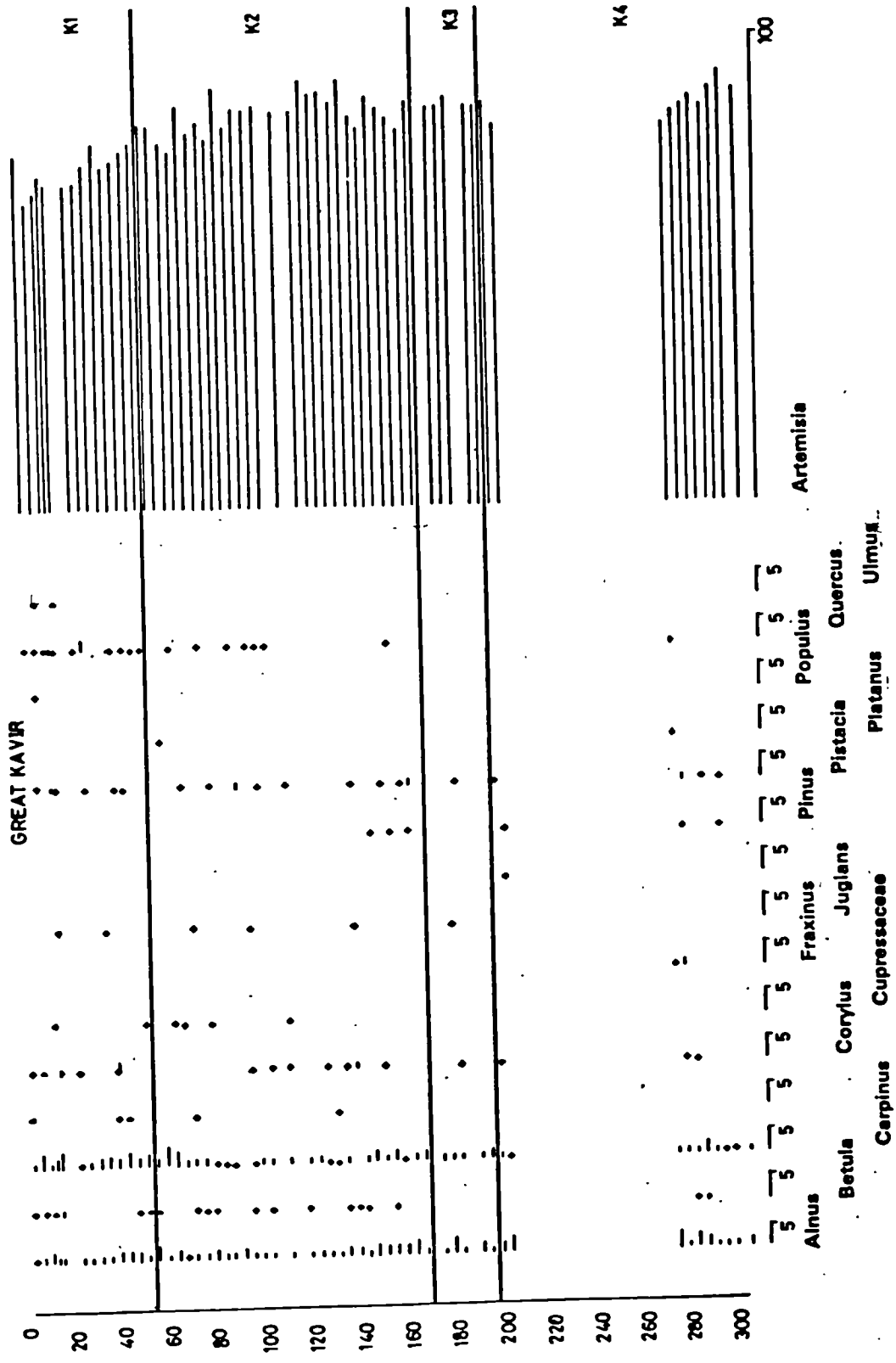

K1
K2
K3
K4
GREAT KAVIR
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
Alnus
Betula
Corylus
Carpinus
Cupressaceae
Cedrus
Fraxinus
Juglans
Pinus
Picea
Pistacia
Platanus
Populus
Quercus
Ulmus
Artemisia

Fig.7.

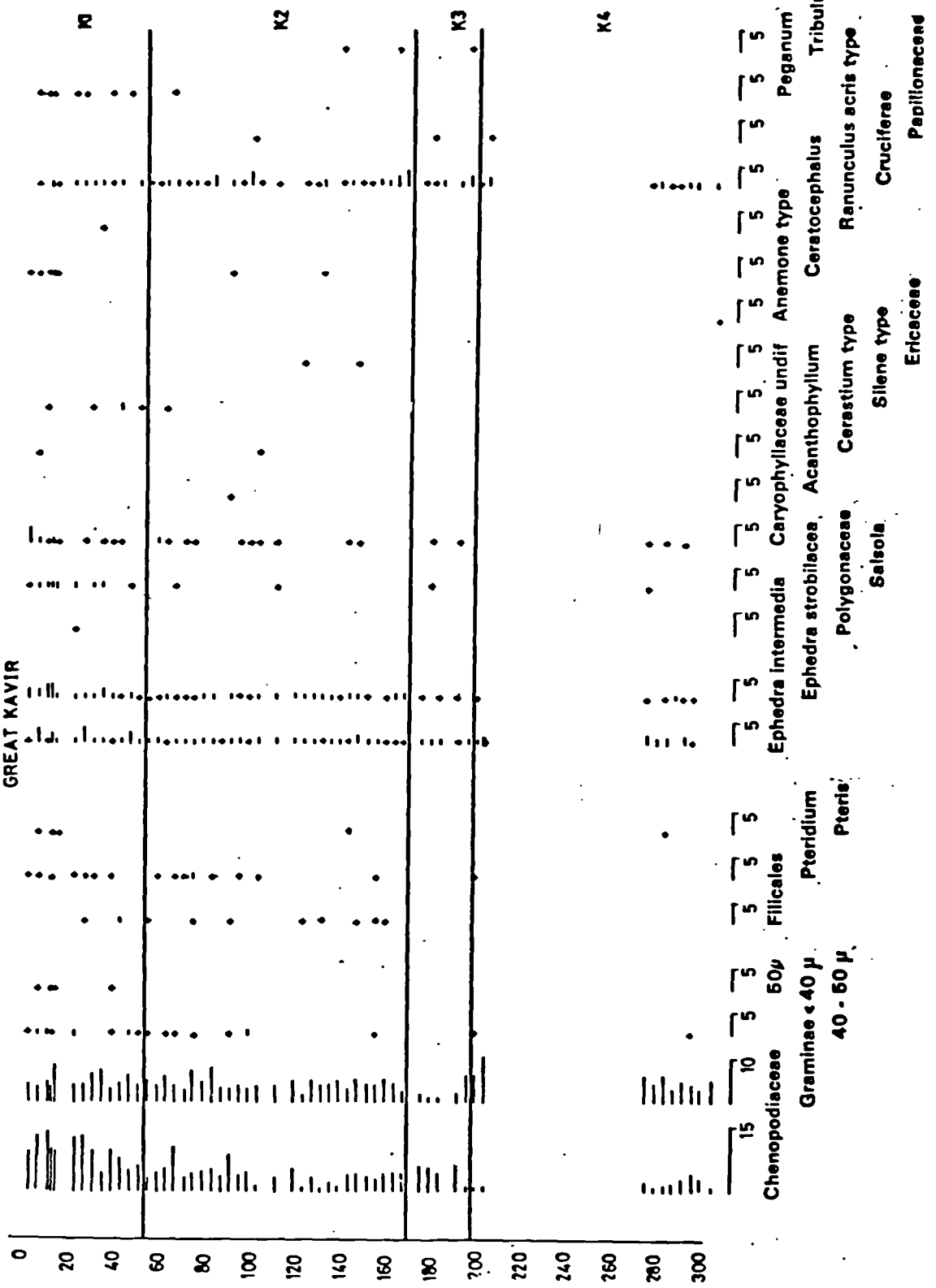
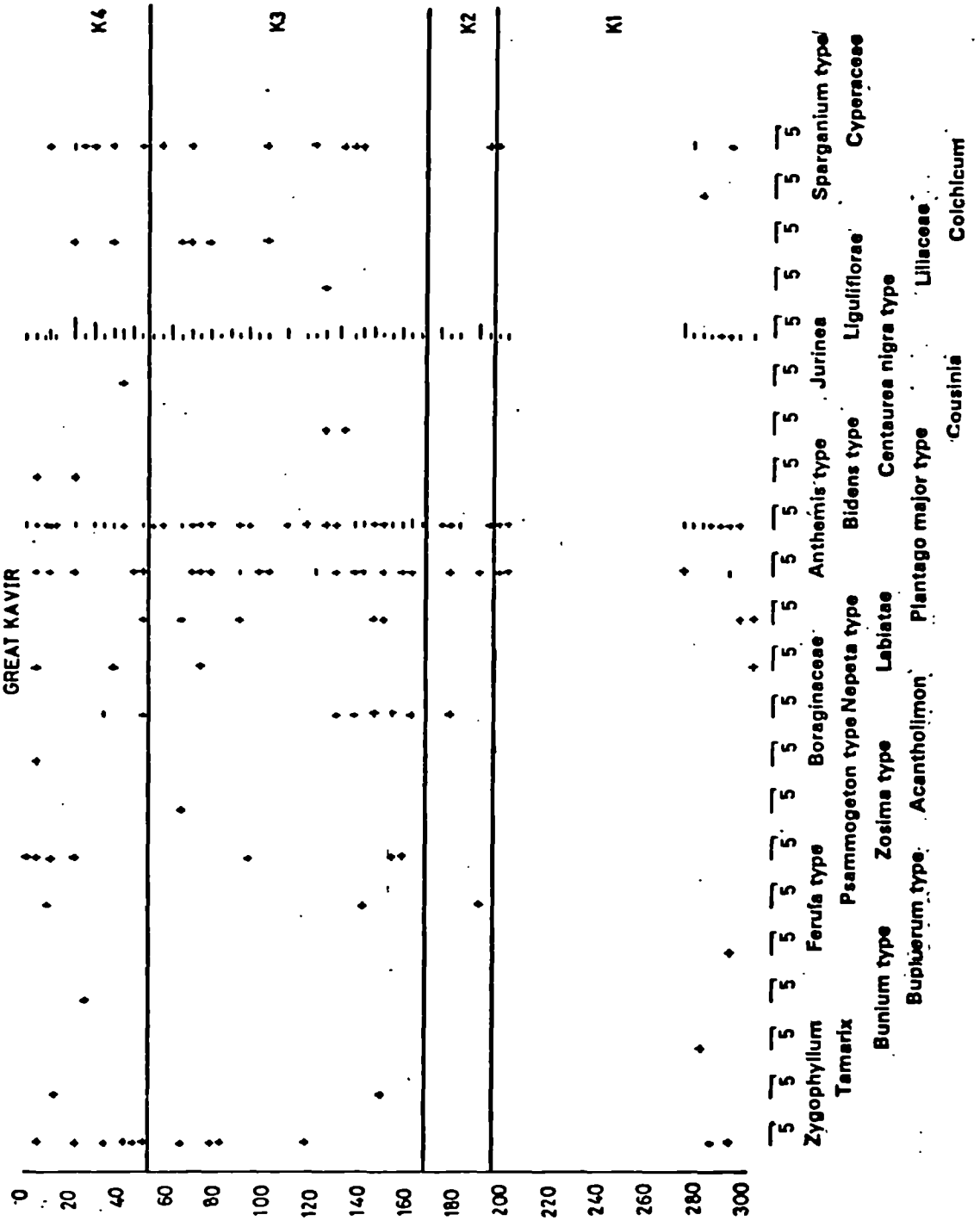

GREAT KAVIR
K1
K2
K3
K4
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
15
10
5
5
5

Fig.9.


GREAT KAVIR
K4
K3
K2
K1
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
Zygophyllum
Tamarix
Bunium type
Bupleurum type
Ferula type
Psammogeton type
Zosima type
Acantholimon
Boraginaceae
Nepeta type
Labiatae
Plantago major type
Anthemis type
Bidens type
Centaurea nigra type
Cousinia
Jurinea
Liguliflorae
Liliaceae
Sparganium type
Cyperaceae
Colchicum

total pollen. No wood or other organic, macroscopic material was found in the excavated section and the organic contant of the sandy sediment was low, consequently it has not been possible to obtain radio-carbon dating for the profile.

The overall uniformity of the pollen data with depth is striking, but certain changes in the profile are evident which permit a tentative zonation. The main features of the zones are:-

K1 Artemisia

Local pollen assemblage zone, 302-194cm.

Very high Artemisia, but low Chenopodiaceae especially in the upper part

K2 Artemisia - Chenopodiaceae

Local pollen assemblage zone, 194-164cm.

Marked by an abrupt rise in Chenopodiaceae and a concomitant fall in Gramineae. Artemisia remains steady

K3 Artemisia

Local pollen assemblage zone, 164-50cm.

Gramineae recover almost to former level. Chenopodiaceae fall gradually but rise again gradually later in the zone. Fern spores appear and Pteridium becomes a regular member of the assemblage, as does Quercus. Artemisia remains fairly steady through most of the zone, possibly declining slightly near the top.

K4 Artemisia - Chenopodiaceae

Local pollen assemblage zone, 50-0cm.

Artemisia shows a distinct decline through this zone apart from the top sample (in which an anther of Artemisia was found). Chenopodiaceae rise to their highest levels. Gramineae > 50μ are present which is suggestive of cereals. Ephedra and Salsola type become generally more frequent, as do certain other types such as Silene type, Cerato-cephalus type and Peganum.

Interpretation of this profile is difficult even with the aid of the modern pollen rain data. The lower diversity of pollen taxa in the lower layers is very striking and may be due to the effect of differential survival (Havinga 1959). This however, is unlikely, since some delicate pollen types such as Pistacia have survived even near the base. Also there are changes in the proportions of the more robust and easily recognisable taxa, such as Artemisia and Chenopodiaceae, which are unlikely to have suffered in this way.

Zone K1 is dominated by high Artemisia and low Chenopodiaceae. The Artemisia values of about 82% are far higher than any found in the surface sample study. This may indicate a larger population of Artemisia plants present at that time, since in the surface samples it was found that only a few plants were needed to provide 60% of the pollen rain and in order to raise this percentage even further, the number of plants had to be in their hundreds. The Chenopodiaceae values are also low, which is contrary to the present day in all sites, and may be due to a lesser abundance of the chenopods at that time. Gramineae are also high compared to present day and are more like the values obtained from

surface samples in Western Iran by Wright et al (1967). Thus it may be that grass populations were also high during this period and have decreased since then. Zygophyllum was also found in this zone in very low quantities but, as has been noted in the surface samples, one must assume that Zygophyllum is grossly under-represented. Therefore, one must consider the possibility that Zygophyllum was of great importance in the surrounding communities. The likely origin of the tree pollen input has already been discussed in relation to the modern pollen results obtained from the area. The points made there are applicable here, and there is no evidence of more extensive forest in the period represented by Kl than at the present day.

The pollen input of the core is mostly associated with the fluviatile inwash from the surrounding hills and slopes (since anthers of Artemisia were found), thus the C_{sf} component of the pollen rain must have been of great importance. A direct aerial input is also occurring but long distance pollen derived from fluviatile inwash will be greater. If this were so, then once again the problem of the low chenopod values is particularly interesting, for the inwash would today have to pass through a chenopod dominated band of vegetation before reaching the Kavir and this, as we have seen from the modern pollen rain, is dominated by Chenopodiaceae pollen. This should result in a large chenopod pollen input into the Kavir, however, the input into the surface level of the core is also low, thus it seems that Chenopodiaceae pollen is not exported from the sites of production.

Zone K2 is marked by a rise in the chenopods and a concomitant fall in the Gramineae. Again Artemisia values are still higher than today, suggestive of higher populations than at present. The fall in Gramineae and rise in chenopods could be explained by overgrazing, reducing the flowering potential of the Gramineae, if not their total populations, and ruderal members of the Chenopodiaceae moving in. A rise in salinity might also cause the chenopods to rise but would not necessarily reduce the Gramineae at the same time. No Peganum which is a good indicator of overgrazing and human influence on the vegetation was found in this zone, however, some grains of Tribulus were found, and this is a plant indicative of disturbed ground. One might also expect pollen of Leguminosae/Astragalus type to increase since it is observed that under grazing Artemisia gives way to tragacanthic Astragalus bushes. But as has been shown from many studies of the Leguminosae, in general they are grossly underrepresented (see Part B of thesis). Again the Artemisia populations may be affected by this overgrazing/human disturbance but, as has already been shown, the values are very insensitive to small changes in population. Again, just because no Zygophyllum was found, does not necessarily indicate it was absent.

Zone K3 is characterized in the early part by chenopods declining and the Gramineae recovering. This may have been caused by the removal of the grazing/human disturbance factors enabling the Gramineae to recover. The chenopods do recover, however, in the later part of the zone and here may represent increasing salinisation of the soil, since the Gramineae do not tend to be affected this time as they were

in zone K2 and K3. In the latter part of this zone some interesting changes take place in the long distance transport element of the pollen. Peaks occur in Carpinus, and also Pteridium continues to be present in the profile. The origin of Pteridium and Carpinus is once again thought to have been the Caspian forests since neither grows nearer the site than that area. Thus the increased values could be the result of changing wind patterns altering the amount of pollen blown in from the Caspian or, more likely, the changes are due to disturbance in these Caspian forests. Wendelbo (1976) has observed how Pteridium aquilinum is currently invading clearings in the Elburz forests and Van Zeist et al (1975) in S.W. Turkey have noted that clearing of forest tends to benefit Carpinus if allowed to regenerate. Thus it seems that the peaks of these types may well be correlated with disturbance. Again Zygophyllum is present and we must not underestimate its position in the communities surrounding the Kavir.

Zone K4 is a zone characterized by a steep rise in the chenopods and a fall in Artemisia to values that approximate pollen rain from many of the present day samples. In this zone the rise in Chenopodiaceae is accompanied by a variety of pollen types that are indicative of human activity, such as Ceratocephalus type, Peganum and Gramineae > 50μ. Peganum especially is found extensively around sheep pens and villages, but again the small values recorded give no indication of the plants importance since Peganum is under-represented in the pollen rain, as is Zygophyllum. However, there appears to be a profound change occurring in the profile in zone K4 with the fall in Artemisia from values of about 85%

to 70%. This could indicate a dramatic collapse of the Artemisia populations responsible for providing the pollen input into the site, which could explain the increase in chenopods found in this zone, since they seem to respond to overgrazing positively. Ephedra also increases in this zone and it is known to be poisonous to stock, so again this increase could be a response to a more intensive grazing regime. However, one must allow also for the possibility that the increase in chenopods may have resulted from increasing salinization of the soil, thus extending the belt of chenopod dominated vegetation around the Kavir, through which the C_{sf} pollen component is transported.

It thus seems that in the time during which the upper 50cm of sediment has been deposited, the rate of change in the vegetation (resulting perhaps from intensified land management and pastoral practices by man) has accelerated. That there is some change taking place is in no doubt; the falling Artemisia and rising Chenopodiaceae, demonstrate such a change. Unfortunately, there is no means of knowing the rate of such a change without the aid of absolute dating.

POLLEN STUDIES

IN

SEMI ARID AREAS

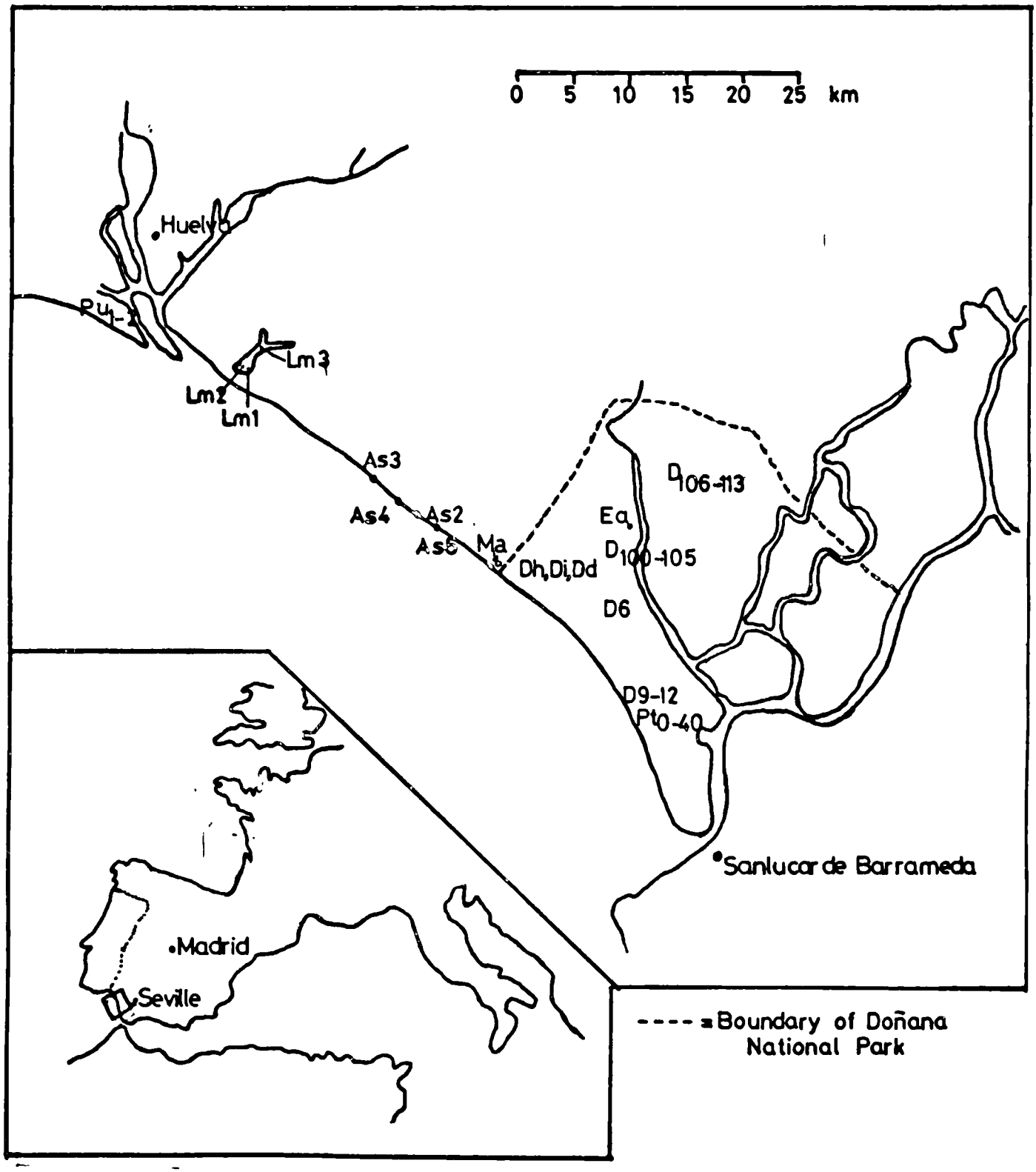
PART B

SOUTH WEST SPAIN

INTRODUCTION

With the termination of the pollen project in North East Iran, it was decided that a similar site in another part of the semi-arid region should be sought in order that some comparison could be made between the two areas in terms of pollen rain and pollen movement. An opportunity then arose to study the past vegetation and modern pollen rain in a semi-arid area of South West Spain, centered on the Doñana National Park. The work contained in this part of the thesis is the result of these analyses. The general area of study will be referred to as "the Doñana area" throughout this thesis.

Fig.10. Map of the Doñana area including core and surface sample sites



CHAPTER 1

Doñana: the Research Area

(i) Geology

The study sites examined in this part of the thesis are all situated in one of the four main geological depressions of Spain, known as the Guadalquivir depression. The depression was caused by subsidence against the hardcore of crystalline and Paleozoic rocks during the alpine upheaval, and extends 320km inland, and is composed mainly of Miocene and Pliocene marine deposits of mark and limestone. To the north is the eroded edge of the crystalline massif and the Sierra Morena, while to the south are more recent Quarternary deposits of fluviatile origin, which were probably washed down from the Sierra Nevada during glaciations in the Pleistocene. In places, fertile terra rossa soils occur as a result of limestone weathering and, with the proximity of the Atlantic moisture, provide rich soils for cultivation. Elsewhere, on siliceous and gypsum soils, cultivation is poor. At the seaward end of the depression lies the marismas, which are extensive, low lying marshes fringed by sand dunes along the coast. See Fig.10 for general map of the area with sites that were analysed during this work indicated.

According to I.G.M.E.(1975) the following geological history holds for the pollen sites bounded by Ayamonte-Huelva map. The sedimentation of a continental platform occurred during the Triassic, which was followed by a marine transgression until Middle/Upper Liassic times. At this time strong differential subsidence of the land with the characteristic of a geosyncline occurred. In the upper Liassic, Jurassic

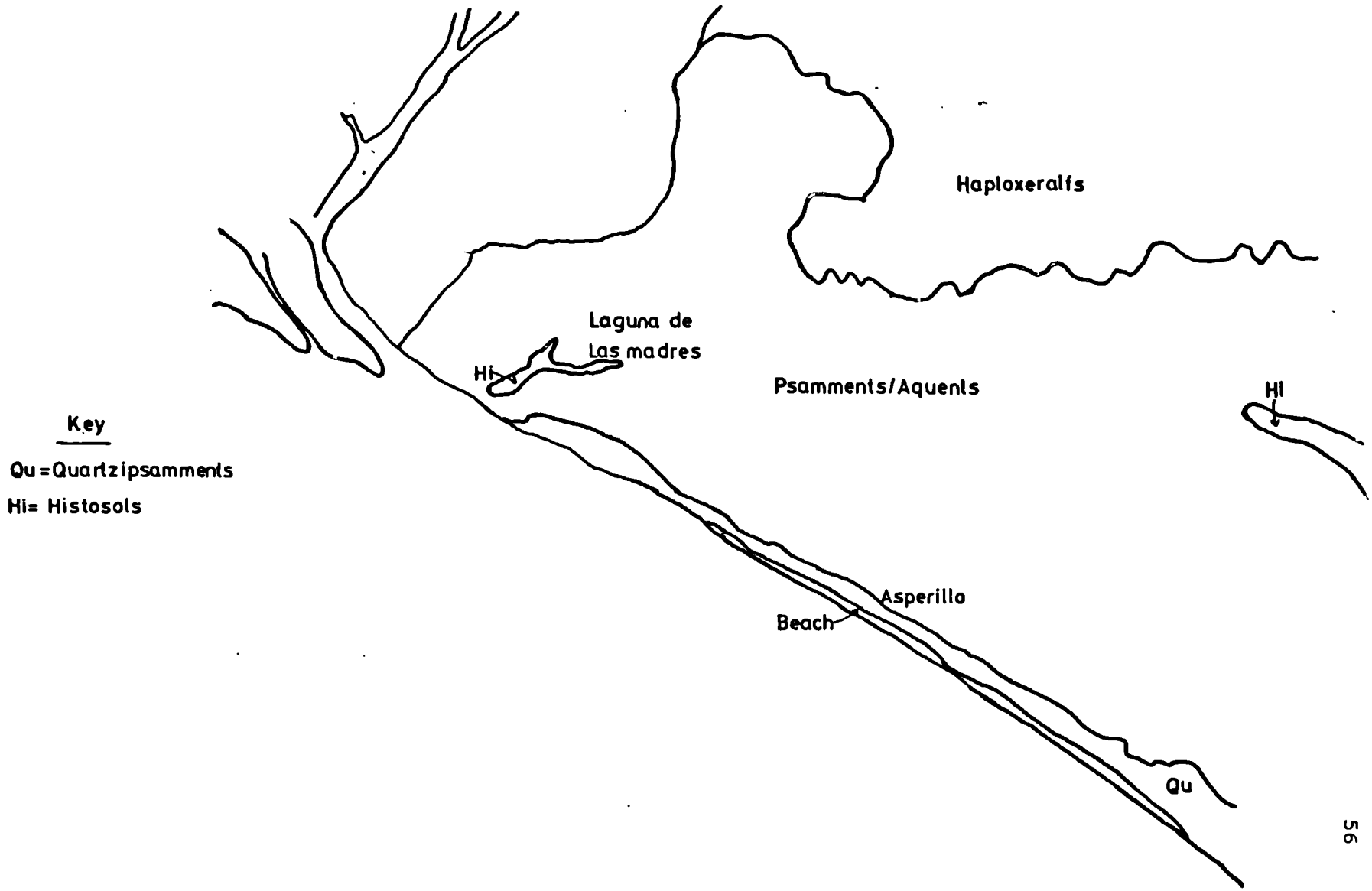
and Lower Cretaceous are again found marine sediments in a typical alpine geosyncline mode. The subsequent geological history is more obscure due to various orogenic events, however, it seems that sedimentation was interrupted in the Middle Cretaceous, only to be resumed as a marine transgression occurred in the Upper Cretaceous.

In the Lower Miocene and possibly late into the Oligocene occurred sedimentation of "Moronitas". Later on, the last of the major faults occurred (Rio Tinto/Odiele). During the late Miocene the area was again under sea and remained so, until a general regression occurred at the beginning of the Pliocene. However, a small marine transgression occurred during the Middle Pliocene, the sea now approached what is now the modern day coast line. The Pleistocene was characterised by extensive deposition of aeolian sands. More important variations in the coastline have continued until the present day, associated with tectonic movements along the European/African plates that meet parallel along the sea separating Europe from Africa.

(ii) Climate

The main type of climate in the Huelva-Seville section of the Guadalquivir depression is mainly Mediterranean, with hot dry summers and moist mild winters. Rainfall throughout the sector is generally low (G. Novo 1979) with Seville having an average rainfall of about 500mm. There is a double maximum in rainfall with 90mm of rain in November/December and a secondary maximum in February/March of 85mm.

Fig.11. **Soil Types of the Doñana area**



Summer drought is severe with no precipitation in July/ August and only 24mm average in June. Summer drought is also coupled with high temperatures (average mean temperatures are for June 20.5°C, July 23.9°C, August 23.6°C). Winters are comparatively mild with average mean temperatures of 9.3°C for the coldest months (January and December). Both maximum and minimum temperatures are milder than is normal, this is due to oceanic influences; temperatures below freezing point are rare. A discussion of the main climatic features of this area may be found in Merino et al (1976). Winds are predominantly onshore, which may have implications for pollen dispersal.

(iii) Vegetation and Soils

Soils of the study area are mostly siliceous (see Fig.11). Consisting of sands deposited during various periods of geological time. To the north exist more calcareous soils on which most of the olive and citrus farming occurs. The siliceous soils not covered either with the original forests or derived shrub communities tend to be planted with either Pinus pinea or Eucalyptus sp. for wood production.

The vegetation of the study area is predominantly of a Mediterranean type. However, because of the Atlantic influence in the area, the vegetation also has an element of plants with an Atlantic distribution e.g. Corema album, Erica vagans, Lygos monosperma. Detailed descriptions of the vegetation in the Doñana area have been carried out by Gonzalez Bernaldez et al (1975 ab), Allier et al (1974). The flora is rich, which may be accounted for in geological terms

by the absence of any permanent ice caps in the South West, which resulted in the survival of a large number of Tertiary species. Also the proximity of Africa has led to some swelling of numbers, and the relative geographical isolation of Iberia has led to a large number of neo-endemics.

The plant communities of the area follow the normal pattern of mediterranean communities (Quezel, 1976). However, the siliceous soils of the area lead to the exclusion of Quercus ilex and Q. rotundifolia and their replacement by Q. suber. There is however, very little of what is thought to have been original mediterranean forest cover left. Only the derived shrub communities are left, caused by the presumed clearance of the trees.

The different types of vegetation occurring on the siliceous soils are controlled by two factors:-

i) Depth of the water table

ii) Stability of the soil

Different combinations lead to different vegetation types. Further more detailed discussion of the vegetation is contained in Chapter 2.

iv) Influence of Man

As has already been noted, very little of the original Mediterranean forest now exists, due mainly to the activities of man. According to G. Novo (unpub.) the history in the Iberian peninsula is as follows. Neanderthal man of the

Mousterian culture was present 100,000-50,000 B.C., and these people gave way to an Upper Palaeolithic culture that left many cave paintings. These were followed 8,000 B.C. by Mesolithic people who gave way 5,000 B.C. to people of the Neolithic cultures. Megalithic people took over about 2,500 B.C. and gave way to Bronze age people around about 2,000 B.C. The beaker people arrived in about 1,000 B.C. and founded a large trading settlement in the Guadalquivir river, known as Tartessus, a city that has long been sought after and has recently been discovered (Menenteau 1981). Phoenician cultures arrived and were followed by trading with the Greeks. Around 500 B.C. the country was populated by people of the so called Iberian cultures that are thought to have a North African origin. Romans invaded the peninsula in 218 B.C. and held it until the collapse of the Roman Empire in 409 A.D. When the peninsula was over-run by the Visigoths, who subsequently in 711 A.D. were invaded by the Muslims, who established a settled culture for 700 years. These cultures were finally ejected by Christians from their last stronghold in Granada in 1492. During all this time each culture was affecting the vegetation in many different ways, including the introduction of new crops into the peninsula: the Bronze and Iron age cultures in particular developed a great potential for cultivation. A detailed history of the recent past in the Doñana area has been conducted by Granados Corona (1980) parts of which will be discussed in subsequent chapters.

v) Past Pollen Studies

Very little pollen analytical work has been conducted in South West Spain, apart from a core analysed from Laguna de las Madres by Menendez Amor and Florschutz (1964) and a preliminary investigation of peat bands in a series of old sand dunes known as "Arenas Gordas" at El Asperillo (Caratini and Viguier 1973).

It was decided to analyse further material from Laguna de las Madres for three main reasons:- a) it was suspected that some misidentification had occurred in prior analysis, b) there was a large residue of unidentified pollen in the published accounts of these analyses, which suggested that much further ecological information could be gained, and c) the site was under threat of peat exploitation, hence further opportunities for re-examination of the site were precluded. It was also decided to widen the investigation to peat bands exposed in the coastal, sandy cliffs of Asperillo, for these bands were known to have been laid down before the formation of peat in Laguna de las Madres. It was thought that this site might provide vegetational history prior to that of Laguna de las Madres. A site in the Doñana National Park was also included, in order to determine whether the remnant of Quercus suber forest present here was natural or planted. To complement all the above studies, it was also decided to conduct modern pollen rain studies in most of the plant communities now extant in the Doñana area.

CHAPTER TWO

The Vegetation and Modern Pollen Rain of the Doñana area

Vegetation of the Doñana Area

The vegetation of the Doñana area has been extensively studied and has been analysed by multivariate analysis (G. Novo et al 1975 and Gonzalez Bernaldez et al 1975b). It has been found that it can be divided into three main types.

1) Vegetation of the stablized dunes
2) Vegetation of the mobile dunes
3) Vegetation of the Marismas

1. Vegetation of the stablized dunes

The vegetation of the stablized dunes has further been subdivided and it is this type of vegetation that dominates the Doñana area. The type of vegetation depends mainly on the depth of the water table and secondarily upon grazing and human influences. A summary table of the effect of water table and succession is seen in Table 3 after G. Novo (1979).

As can be seen from the table, four main types of vegetation exist at each stage in the successional process. A detailed description of each type now follows:-

A. Grassland systems

This type of system is normally found under conditions of high grazing intensity (e.g. by Sus sofra and Cervus sp.) and also trampling on the coastal sand dunes near large conurbations. The dryest grassland system has Loeflingia baetica and Tuberaria guttata well represented. As the water table nears

TABLE 3

Scheme of vegetation composition changes as a function of two factors: average water table depth (in columns) and succession stages (in rows) in Doñana area

Depth of water table		Types of vegetation		
Winter	Summer	Grassland	Shrub	Forest
2 to 3 m	over 3 m	Malcomia lacera Brassica barrellieri Linaria viscosa Loeflingia baetica Tuberaria guttata	Cistus libanotis Lavandula stoechas Halimium commutatum Thymus mastichina Helichrysum angustifolium Halimium halimifolium	Juniperus phoenicia Pistacia lentiscus Osyris quadripartita Quercus coccifera
1 to 2 m	1.5 to 3 m	Agrostis stolonifera Holoschoenus vulgaris Hypericum tomentosum	Halimium halifolium Stauracanthus genistioides Calluna vulgaris Erica scoparia	Quercus suber Arbutus unedo Olea europaea Phillyrea angustifolia
0 to 0.5m	0.5 to 1.5 m	Mentha pulegium Hypericum tomentosum Anagallis crassifolia Illecebrum verticillatum Armeria gaditana Agrostis stolonifera Eleocharis palastris	Ulex minor Erica ciliaris Erica scoparia Erianthus ravennae Imperata cylindrica	Quercus suber Arbutus unedo Pyrus bourgeana Fraxinus angustifolia Myrtus communis Phillyrea angustifolia
-1 to 0 m	0 to 0.5 m	Echinodorus ranunculoides Hydrocotyle vulgaris Ranunculus sec. Batrachium Carex spp.	Juncus spp. Typha latifolia	Populus alba Tamarix africana Tamarix canariensis

Increased depth of water table in the soil

Succession ⟶

the surface Holoschoenus vulgaris and Agrostis stolonifera become dominant. A wetter variant still, has Illecebrum verticillatum, Armeria gadiatana and Eleocharis palustris frequent. The wettest variant is dominated by Echinodorus ranunculoides, Hydrocotyle vulgaris, Carex sp. and Ranunculus sp.

B. Shrub Systems

i) Monte blanco shrub communities

This represents the dryest of the four shrub types. The water table in summer is over 3m deep. Little soil development occurs and neither horizons of eluviation or accumulation can be observed. The pH of the soil is 5.5 and the sand surface, because of the lack of soil development, is yellowish/orange in contrast to the grey white soils of the monte negro communities. The plants that dominate the community are Cistus libanotis, Lavandula stoechas, Rosmarinus officinalis, Halimium commutatum and H. halimifolium.

ii) Monte negro shrub communities

The depth of the water table in this shrub type is less than in the previous community with a depth of about 1.5-3m in summer. Some soil development has occurred giving rise to a white/grey soil (indicative of oxide reactions) with a definite organic hotizon. Plants characteristic of this community include Stauracanthus genistioides, Calluna vulgaris, Erica scoparia, Halimium halimifolium.

iii) Monte negro hygrophytic shrub communities

This is the wettest of the shrub types with the water level at or near the surface during the winter. Soils are high in organic matter with marked gley horizons. In these communities Erica scoparia is the dominant shrub and plants that are not able to withstand water stress occur, e.g. Erica ciliaris, Ulex minor, Erianthus ravennae and Imperata cylindriea. Plants characteristic of shrub types i) and ii) are normally absent from this shrub type due to shading, unless openings occur in the canopy.

iv) Typha/Juncus communities

These communities develop in situations where the water level is very high, where even during the summer the level is 0-0.5m and is characterized by extensive flooding in the winter. The high water level prevents development of the more normal shrub systems, e.g. monte negro hygrophytic.

C. Forest Systems

If the four main types of shrub community are allowed to develop without the influence of fire or man, then they will develop into four derived forest communities. Once again the depth of the water table is of prime importance in determining the type of forest.

i) Monte blanco forest

The dryest of the shrub types if left undisturbed will develop into Juniperus phoenicia dominated forest. On the more silty soils Pistacia lentiscus becomes very common. The parasite Osyris quadripartita is also

associated with these communities. In rare sites the "kermes oak" Quercus coccifera also occurs. On the more oceanic sites J. phoenicia eventually gives way to a forest dominated by J. oxycedrus.

ii) Monte negro forest

This is a forest type derived largely from monte negro shrub vegetation. Common plants are Olea europaea, Quercus suber. Other associates are Phillyrea angustifolia and Arbutus unedo. This acidophilic, thermophilous forest is nowadays restricted to a small portion in the north of the Doñana National Park. It is thought that Ceratonia siliqua was also a component of this forest type; nowadays this tree is restricted to the Eastern Mediterranean.

iii) Monte negro hygrophytic forest

This wetter variant of the monte negro forest loses the more thermophilous element of Olea europaea and becomes dominated by Quercus suber. Other plants intolerant of water stress occur, such as Myrtus communis, Pyrus bourgeana. Arbutus unedo is a common understorey shrub in these forests, and the forest also carries a heavy impenetrable liana component of Smilax aspera, Rubia peregrina and Lonicera pericylmenum. In the wetter hollows a different variant of the forest develops which is dominated by Fraxinus angustifolia with Vitis vinifera as a liana.

iv) Tamarix communities

The wettest of the four shrub communities that are domiated by Typha latifolia and Juncus sp. often

develop into a forest dominated by Tamarix africana, T. canariensis and Populus alba. An intermediate stage between this community and the wetter variant of the last community contains Tamarix africana and Fraxinus angustifolia.

2. Vegetation of the Mobile Dunes

Systems of this kind are found nowadays in the south of the Doñana National Park. They are characterised by extensive fronts of transgressive dunes (Ranwell 1972) that move across the intervening slacks at a rate of 5-6m yr^{-1}. Substrate mobility is the controlling factor in determining how long the succession lasts in the slack. The depth of the water table once again determines the type of vegetation that can develop, i.e. monte blanco etc. as on the stabilised dunes. However, because the dune fronts are moving, the succession is likely to be terminated early on, preventing the system from developing into forest. The monte blanco slacks have developing in them a forest dominated by Pinus pinea (G. Novo 1979). Detailed vegetation analyses of the mobile dunes are given by Allier et al (1974), G. Novo et al (1975) and G. Novo (1979). A summary of the main vegetation types will now be given. See also the summary table (after Allier et al 1974).

A) Dunes

The substrate is very unstable in these situations and the depth of the water table is greater than 4m. The following vegetation develops in such conditions, e.g. Dune fronts and dune tails.

TABLE 4

STABILITY OF THE SUBSTRATE

Schema of the variation of the vegetation of dunes and slacks as a function of the substrate mobility and depth of the water table. Only the characteristic species are given.

Dunes

Sand very mobile and tails of dunes. (Velocity of sand movement 4.5m yr^{-1}). Depth of water table >4m.

Ammophila arenaria
Cyperus schoenoides
Echium gaditanum
Rumex tingitanus
Corema album
Helichrysum italicum
Stauracanthus genistioides
Juniperus phoenicea
Pistacea lentiscus
Phillyrea angustifolia
Osyris quadripartita
Cytisus grandiflorus

Slacks

Sands less mobile, first contradunas, dry slacks with vegetation of monte blanco type. Depth of water table >2m.

Armeria pungens
Artemisia campestris
Carex arenaria
Scrophularia frutescens
Pinus pinea (jovenes)
Halimium halimifolium
Halimium commutatum
Stauracanthus genistioides
Pinus pinea
Halimium halimifolium
Halimium commutatum
Stauracanthus genistioides
Lavandula stoechas
Thymus mastichina

TABLE 4 cont.

Humid slacks with vegetation of monte negro type

Depth of water table, Winter 0.5-1m, Summer 1-1.5m.

Pastizal	Matorral
Agrostis stolonifera	Halimium halimifolium
Holoschoenus vulgaris	Calluna vulgaris
Hypericum perforatum	Erica scoparia
Panicum repens	Stauracanthus genistioides
Centaurea melitensis	

Humid slacks with vegetation of monte negro hygrophytic type

Depth of water table, Winter 0-0.5m, Summer 0.5-1m.

Agrostis stolonifera	Calluna vulgaris
Armeria gaditana	Erica scoparia
Anagallis crassifolia	Erianthus ravennae
Eleocharis palustris	Ulex minor
Mentha pulegium	
Cotula coronopifolia	

Slacks, temporarily flooded, without mattoral

Depth of water table 0-0.5m

Echinodorus ranunculoides	Juncus spp.
Carex distans	
Glyceria fluitans	
Hydrocotyle vulgaris	
Ranunculus baudotii	

Table 4 shows the main vegetation characteristics of the mobile dunes. At first the substrate is colonised by Ammophila arenaria and Cyperus schoenoides, Echium gaditanum and Rumex tingitanus. A shrub development can take place if the sands stabilise slightly with invasion by Corema album, a plant that can withstand a degree of substrate mobility. A forest type can develop much as in the stabilised sand dunes, and with the water table over 4m down this forest is made up of typical monte blanco forest species. This situation is rarely reached in the modern day sites in the Doñana National Park.

B) Dune Slacks or "Corrales"

Four main types of vegetation can develop in the dune slacks, the determining factor being the depth of the water table.

Throughout the slacks occur structures known as contradunas (Allier et al 1974), which originate because of winds that are inverse to the dominant wind, blowing during sufficiently long dry periods. In the slack, these contradunas become fixed with vegetation. These contradunas have an effect on the vegetation in delimiting microclimates within the slack system of xerophytic sites and hygrophytic sites. Once stabilised the contradunas do not shift, thus the base of the slack becomes occupied by a series of immobile contradunas between two large mobile dunes.

i) Monte blanco type slacks:- Water table < 2m.

The vegetation of these communities is characteristically found on the more stable substrates, just after the slack is being formed by the retreating tail of the

dune and also of the first contradunas formed in the slack. This type of vegetation is also found in slacks where the water table is greater than 2m. A summary of the main vegetation components of these conditions is given in Table 4. The first plant invaders are normally Artemisia campestris and Carex arenaria. As the succession progresses these are replaced by shrubs of Halimium sp. and an invasion by Pinus pinea. A forest development can then take place, with Pinus pinea being dominant. This forest type is not to be found in the stabilised dunes, because of the short lifespan of the slack (approximately 40 years), which only Pinus pinea can colonise the slacks, grow and produce seed in the timescale, and thus keep up with the advancing dune fronts. Normally in the Mediterranean region, Pinus is replaced by Juniperus (Harrant and Jarry 1967), however, Juniperus needs a longer timescale to complete its life-cycle and therefore is prevented from invading the Pinus forest. Pinus pinea is prevented from invading the wetter slacks and the slacks between contradunas because its roots are susceptible to waterlogging. Thus the distribution of Pinus pinea has been found to be contagious in the dune slack systems, with the tree restricted to the contradunas (Figueroa 1976).

ii) Monte negro type slacks

This vegetation develops in the wetter slacks and the shrub component resembles that seen in the stabilised dune systems. The initial stages of colonisation are slightly different, with a flora of Agrostis stolonifera and Holoschoenus vulgaris being very common.

Forest development is precluded due to the short timescale of the slack. The slack being too wet for invasion by Pinus pinea.

iii) Monte negro hygrophytic slacks

Once again the shrub development resembles that seen in the same situations in the stabilised sand dunes, i.e. Erica scoparia, Calluna vulgaris. The initial stages are characterised by wetter plant indicators such as Eleocharis palustris.

iv) Temporary lagoons

Echinodorus ranunculoides and Carex distans are the main colonisers of these lagoons. The shrub type being represented by Juncus sp.. These lagoons often form as the next dune front approaches (G. Novo 1979). It is noticeable that Typha latifolia does not appear to be a constituent of these temporary lagoons as it is in the stabilised sand dunes.

3. Marsh vegetation

The marsh vegetation is dominated by Scirpus lacustris in the wetter areas of the marsh, with S. maritima being the dominant plant found elsewhere. The characteristic chenopod vegetation of many brackish marshes is not found in the Doñana National Park, but does exist on other marshes in the Doñana area. A detailed discussion of the vegetation of the marsh communities may be found in Allier et al (1974)

Modern Pollen Survey of the Vegetation Communities of the Doñana area

Methods

A modern pollen survey of most of the vegetation types just described was conducted in order that the results could be related to the data obtained from the fossil pollen cores. Very little research has been conducted into the modern pollen rain of Mediterranean communities with most of the work being confined to the Eastern Mediterranean, e.g. Bottema and Barkoudah (1979) in Syria, Van Zeist et al (1975) in S.W. Turkey. Studies relating to the Western Mediterranean are confined largely to the studies of Reille (1975) in Corsica and Beaulieu (1977) in the French Alps. In general there is a paucity of information about modern pollen rain in Mediterranean communities.

The following pollen survey involved the analysis of surface pollen samples from ten community types (nomenclature follows Flora Europaea). Only the most important species are mentioned; further information is to be found in the original vegetation descriptions and in the tables of vegetation from the sample quadrats (Tables 5-8).

Two methods of sampling the vegetation were used:-

i) 10m x 10m quadrats

ii) Line transects sampled at regular intervals

For the majority of sites selected for the analysis, a sample

area was located in the centre of an extensive stand of uniform vegetation. The areas were chosen on the basis of previous multivariate analysis of the vegetation (G. Novo 1979), so as to get a representative selection of the main vegetation communities of the area. Within the sample area a 10m x 10m square was marked out and all the perennial shrubs and trees counted. The perennial herbs were normally assessed on the Braun-Blanquet cover index scale. Other species not in the quadrat but in the vicinity were listed separately.

In some of the vegetation types, e.g. Pinus plantation and a Quercus suber wood a line transect method was used to sample the vegetation. The rationale behind this being to study the effects of moving from one vegetation type to another, on the dispersal and pollen representation of the tree species involved. The line was laid out from the centre of the Pinus plantation and run out on to the surrounding grassland. The Quercus suber wood was sampled by running a transect from monte negro hygrophytic shrub vegetation into the wood and out again on to a monte negro shrub community. A transect was also used in the mobile sand dunes and was sampled every 5m (sites Pt 0-45). Samples were taken every 20m along each transect by setting up a 10m x 10m quadrat at each 20m and, analysing the vegetation as has just been described.

From within the 10m x 10m quadrat used in both methods, ten surface samples of surface sand with its content of organic matter were collected, each sample being of about $5cm^3$ in

volume. These were mixed thoroughly together and transported and stored in sealable polythene bags. A single sample of approximately $1cm^3$ was eventually used for pollen analysis. The rationale behind this sampling method has been given in part A of this thesis (p.18). The following communities were sampled:-

i) Monte blanco shrub communities

This community is characterised by low water tables and stable sands. Common plants were Cistus libanotis, Rosmarinus officinalis, Lavandula stoechas, Halimium commutatum and H. halimifolium. Four samples were taken from this community - Dd1, Dd2, Dd3, Dd4.

ii) Monte negro shrub communities

These communities influenced by a higher water table than in i) again had Halimium sp. and Rosmarinus officinalis present but very little Cistus libanotis. Other important components were Stauracanthus genistioides, Calluna vulgaris and a little Erica scoparia. Four sites again were examined - Dx1, Dx2, Dx3, Dx4. Dx1, Dx2 and Dx4 were from a mature community. Dx3 was from a regenerating community that had been disturbed by fire.

iii) Monte negro hygrophytic shrub communities

This system which has a high water table is dominated mainly by Erica scoparia and Erianthus ravennae. Five sites were examined - Dh1, Dh2, Dh3, Dh4, Dh5. Dh1, Dh3, Dh5 were all from a mature section of the shrub, Dh2 was from a portion undergoing regeneration and Dh4 from the grazing derived grassland system of the monte

negro hygrophytic shrub communities.

iv) Monte blanco forest communities

These sites in direct line of succession from the monte blanco shrub communities were dominated by Juniperus phoenicia and J. oxycedrus. Two sites were examined from this community:- Pul, Pu2.

Sites were also examined from the monte blanco communities that develop on the more silty soils, i.e. those dominated by Pistacia lentiscus. Phillyrea angustifolia was a common component of these samples and was always found growing within a bush of Pistacia Four samples were collected - Dl06, Dl07, Dl08,Dl09. Dl06 and Dl07 were from the last surviving bushes left in the south of the Doñana National Park, while Dl08 and D 109 were from an extensive Pistacia dominated community in the north of the Doñana National Park known as the "Coto del Rey".

v) Monte negro forest community

This intermediate stage existing between the dryest and wettest of the forest communities becomes dominated by Olea europaea and Quercus suber. One site was examined from such a community - Dll0.

vi) Monte negro hygrophytic forest communities

The climax of this vegetation type is dominated by Quercus suber, Arbutus unedo and heavy liana populations such as Smilax aspera. Seven sites were examined by a line transect method. The transect ran from a monte negro hygrophytic shrub community into the derived forest dominated by Quercus and out again into a monte

negro shrub community. The seven sites in order were D100, D101, D102, D7, D103, D104, D105 at 20m intervals.

vii) Fraxinus/Tamarix communities

This system, a wetter variant of community vi) is found in the Coto del Rey of the Doñana National Park. Three sites were examined - D111, D112, D113. D113 also had a dense growth of Vitis vinifera.

viii) Mobile dune vegetation

Several sites were examined with respect to substrate stability. The first sites were from one of the dune slacks in the mobile dune system of the Doñana National Park. Four sites with a predominance of Pinus pinea were examined - D9, D10, D11, D12. A transect was also taken from a Pinus dominated ridge of one contraduna across its slack dominated by Holoschoenus vulgaris and onto the Pinus dominated ridge of the next contraduna. These sites were Pt0-Pt40 and were sampled at 5m intervals.

One site was also examined from the top of a semi immobilised dune at El Asperillo which was dominated by Corema album - As1.

Three more sites were examined from a more stable dune slack system situated close to Matalascañas. This system, where stability had been enough to allow colonisation by Juniperus phoenicia and J. oxycedrus was also dominated by Corema album and Urginea maritima and many herb species. The sites were Ma1, Ma2, Ma3.

ix) Pinus pinea plantation

This community was sampled by means of a line transect every 20m and ran from within the plantation out onto the grassland and marsh surrounding the plantation at Laguna de las Madres. The sites were Lm1-Lm5.

x) Eucalyptus plantation

One site was examined from a Eucalyptus plantation in the Doñana National Park - D6.

All the samples were brought back to London by plane and stored at 2°C until required for preparation. The pollen extraction method follows that described in Appendix B, but with an HF phase of four hours. In general 500 land pollen grains were counted from each site using Zeiss phase contrast microscope with x40 and x100 lenses. Pollen was identified using keys given in Moore and Webb (1978), except for types not found in this key, where a set of keys were constructed including most of the common Mediterranean plants (Appendix A). Type material was collected from the area or taken from herbarium material from the European herbarium of the British Museum. A type collection of over 1,500 mediterranean plants was made from these sources and with a type collection of most of the N. European plants over 3,000 slides were available for pollen identification. Further details of pollen identification and keys to the families will be found in Appendix A.

The results of the modern pollen survey have been presented in the form of a conventional pollen diagram. In that it was thought that this would lead to easier comparison between

the plant communities than if they were presented in conventional tabular form. Each line represents a particular sample and has a sample identification label associated with it. All the samples are broadly grouped into the community types just described. The pollen diagrams are given in Figs. 12-22, and a generalised map of the area showing locations of modern pollen samples and fossil cores may also be consulted (Fig.10). The vegetation results of each sample are given in Tables 5-8. The pollen sum used for expression of the results is as follows:- Every type except for the Cyperaceae and Aquatic plants are expressed as a percentage of the total pollen minus these two components, i.e. % of the total land pollen. The aquatics are expressed as a percentage of the total pollen minus Cyperaceae, while the Cyperaceae are expressed as a percentage of the total pollen.

VEGETATION TABLES

Tables 5-8 present the plant counts for the surface sample pollen counts. The following key is applicable to these tables.

1. 1, 2, 3 etc. refer to actual plant numbers per 10m x 10m quadrat.
2. $+^n$, where n = 1-5 refers to estimate of plant cover on the Braun-Blanquet scale in cases where no accurate density count could be made (applies only to dwarf shrubs).
3. +, where recorded for dwarf shrub species is equal to the + of the Braun-Blanquet scale, i.e. < 1% cover and scattered.
4. +, where recorded for herbs, gives just presence/absence dates, no density Braun-Blanquet readings were obtained.

TABLE 5

	Dd1	Dd2	Dd3	Dd4	Dx1	Dx2	Dx3	Dx4	Dh1	Dh2	Dh3	Dh4	Dh5	D6
Trees & Shrubs														
Cytisus grandiflorus													1	
Eucalyptus														1
Juniperus phoenicia				1										
Myrtus communis									1		1			
Phillyrea angustifolia									1	1				
Pinus pinea									1					
Dwarf shrubs and lianas														
Calluna vulgaris					+1	+1	+1		+1	+1	+1	+2	+1	
Cistus ladanifer												1		
Cistus libanotis	+3	+3	+4		+2	+2	+1							
Cistus salvifolius									+1	+1	+1			
Daphne gnidium											1			
Erianthus ravennae									2	1	1			
Erica ciliaris									+1	+1			+1	
Erica scoparia					+2	+2	+2		+5	+5	+5	+2	+5	
Erica umbellata													+1	
Genista anglica				1				1						
Halimium commutatum	+2	+2	+2		+2	+2	+2	+2						
Halimium halimifolium	+2	+2	+1	+2	+3	+3	+3	+3	+					
Helichrysum italicum	+1	+1	+1											
Lavandula stoechas	+1	+1	+1		+1	+1	+1	+1						
Osyris quadripartita								1						

TABLE 5 cont.

	Dd1	Dd2	Dd3	Dd4	Dx1	Dx2	Dx3	Dx4	Dh1	Dh2	Dh3	Dh4	Dh5	D6
Dwarf shrubs and lianas														
Rosmarinus officinalis	+[1]	+[1]	+[1]		+[1]	+[1]	+[1]	+[1]						
Rubus ulmifolius									+	+				
Spartium junceum								1						
Stauracanthus genistioides					1	1	2	2						
Ulex minor						+	+		+	+	+	+		
Herbs														
Agrostis sp.												+		
Anagallis arvensis									+	+	+	+		
Armeria pungens			+	+										
Carlina sp.							+							
Eleocharis palustris												+		
Frittalaria lusitanica								+						
Hydrocotyle vulgaris												+		
Hypericum sp.												+		
Juncus bufonis												+		
Juncus capitatus												+		
Juncus tingitanus												+		
Leucojum sp.				+										
Loeflingia baetica	+	+	+											
Malcomia littoralis				+										
Mentha pulugeium												+		
Senecio sp.												+		
Thymus mastichana				+										
Tuberaria guttata								+						
Viola sp.												+		

TABLE 6

	Ma1	Ma2	Ma3	Lm1	Lm2	Lm3	Lm4	Lm5	Dl11	Dl12	Dl13
Trees & Shrubs											
Fraxinus angustifolia									3	2	2
Juniperus oxycedrus	1	1									
Juniperus phoenicia	1	1									
Pinus pinea		2	3	2	2						
Pistacia lentiscus						0					
Quercus suber											1
Tamarix africana									2	7	10
Dwarf shrubs and lianas											
Artemisia campestris		+[1]	54								
Chamaerops humilis				0	0	+					
Cistus salvifolius	+[1]	+[1]				0					
Corema album	4										
Genista anglica			2		0						
Halimium commutatum	5	+[1]			+	+					
Halimium halimifolium	1				+	+				1	
Lavandula stoechas		3	7								
Rosmarinus officinalis	1										
Rubus ulmifolius								+			
Spartium junceum		1									
Stauracanthus genistioides						-	0				
Vitis vinifera										-	+

TABLE 6 cont.

	Ma1	Ma2	Ma3	Lm1	Lm2	Lm3	Lm4	Lm5	D111	D112	D113
Herbs											
Anagallis arvensis				+	+				+	+	+
Anthoxanthum sp.						+					
Anthemis sp.	+	+	+								
Anthyllis sp.		+									
Armeria pungens	14		+								
Asparagus aphyllus					+						
Carpobrutus edulis		+									
Cerastium sp.				+							
Corrigiola sp.	+	+									
Corynephorous canescens	+		+								
Cruciferae		+									
Diplotaxis sp.					+						
Echium sp.	+										
Erodium sp.	+	+				-	+				
Holcus lanatus		+									
Juncus acutus								-	+	+	+
Lactuca sp.	+										
Leucojum sp.					+	+					
Linaria sp.		+									
Lupinus sp.		+									
Malcomia littorea			+								
Medicago arabica		+									
Ornithopus compressus					+	+					
Ornithopus perpusillus		+				+	+				
Phragmites australis								+[5]			
Pimpinella sp.					+						
Plantago coronopus					+	+	+				

TABLE 6 cont.

	Ma1	Ma2	Ma3	Lm1	Lm2	Lm3	Lm4	Lm5	Dl11	Dl12	Dl13
Herbs cont.											
Plantago lanceolata					+	+					
Polygonum sp.	+	+							+	+	+
Pteridium aquilinum								+			
Raphanus sp.				+							
Rumex acetosella	+				+	+	+				
Scolymus sp.									+	+	+
Senecio sp.		+							+	+	+
Sherardia arvensis					+	+			+	+	+
Spergularia sp.					+						
Silene	+										
Thapsia villosa	+	+	+								
Trifolium subterranum						+					
Urginea maritima	+	+	+				+	+			
Urtica urens										+	+

TABLE 7

	D9	D10	D11	D12	Pt0	Pt5	Pt10	Pt15	Pt20	Pt25	Pt30	Pt35	Pt40	As1
Trees & Shrubs														
Pinus pinea	1	8	9	1	1	1						1	2	5
Dwarf shrubs and lianas														
Artemisia campestris	+													
Cistus salvifolius														+[1]
Corema album		1												10
Genista anglica		33			2	2					4	5		5
Halimium commutatum														+[1]
Lavandula stoeches														1
Rosmarinus officinalis	+	+												1
Rubia peregrina	+	+												
Rubus ulmifolius						+								
Spartium junceum														1
Ulex minor				+[4]										
Herbs														
Agrostis stolonifera			+	+		+	+	+						
Ammophila arenaria	+													
Armeria pungens		+												
Carex arenaria					+	+			+	+	+			
Cerastium sp.	+													
Corydalis claviculata						+								
Corynephorus canescens	+													
Echium sp.	+													
Erigeron		+	+											

TABLE 7 cont.

	D9	D10	D11	D12	Pt0	Pt5	Pt10	Pt15	Pt20	Pt25	Pt30	Pt35	Pt40	As1
Herbs cont.														
Holcus lanatus				+		+	+	+	+					
Holoschoenus vulgaris	+	+	+	+	+	+	+	+	+	+	+	+		
Hypochaeris glabra	+						+							
Juncus acutus							+	+						
Leontodon sp.						+								
Lotus creticus	+													
Malcomia littorea	+		+											
Rumex acetosella		+									+		+	
Senecio sp.				+										
Silene sp.			+											

TABLE 8

	Pu1	Pu2	D106	D107	D108	D109	D110	D100	D101	D102	D7	D103	D104	D105
Trees & Shrubs														
Arbutus unedo								1		1	1			
Juniperus oxycedrus	4													
Juniperus phoenicia	1	1												
Myrtus communis			1	1										
Olea europaea							1							
Phillyrea angustifolia			1	1	1			1			1			
Pinus pinea		2					1							
Pistacia lentiscus			2	1	3	2	2							
Pyrus bourgeana						1								
Quercus suber						1			1	2	0	2		
Rhamnus lycioides	1	1			1		1							
Dwarf shrubs and lianas														
Cistus salvifolius	+	+		1		1	+							
Daphne gnidium	1			1	1		1							
Erica scoparia			+	+		+		$+^5$	$+^5$	$+^2$				
Genista anglica												-	1	
Halimium commutatum	+													$+^2$
Halimium halimifolium		+					+						$+^3$	$+^3$
Lavandula stoechas													2	3
Lonicera periclymenum											+			
Rosmarinus officinalis	+	+												
Rubus ulmifolius							-	+	+	+	+			
Smilax aspera			-	+				+	+	+	+			
Stauracanthus genistioides							1						2	1

TABLE 8 cont.

	Pu1	Pu2	D106	D107	D108	D109	D110	D100	D101	D102	D7	D103	D104	D105
Herbs														
Agrostis sp.			+	+										
Anthemis sp.													+	+
Asphodelus cerasifer						+								
Bryonia cretica						+								
Centranthus calcitrapa	+	+												
Compositae undif.													+	+
Filago sp.		+												
Holcus lanatus	+													
Juncus bufonis				-	+									
Linaria sp.		+												
Lotus corniculatus	+													
Medicago littorea	+													
Myosotis sp.		+												
Ornithopus compressus		+												
Pteridium aquilinum							-	+	+	+	+	+		
Ruscus aculeatus					-	+								
Scleranthus		+												
Silene sp.	+													
Sonchus sp.		+												
Thapsia sp.		+												

Fig.12

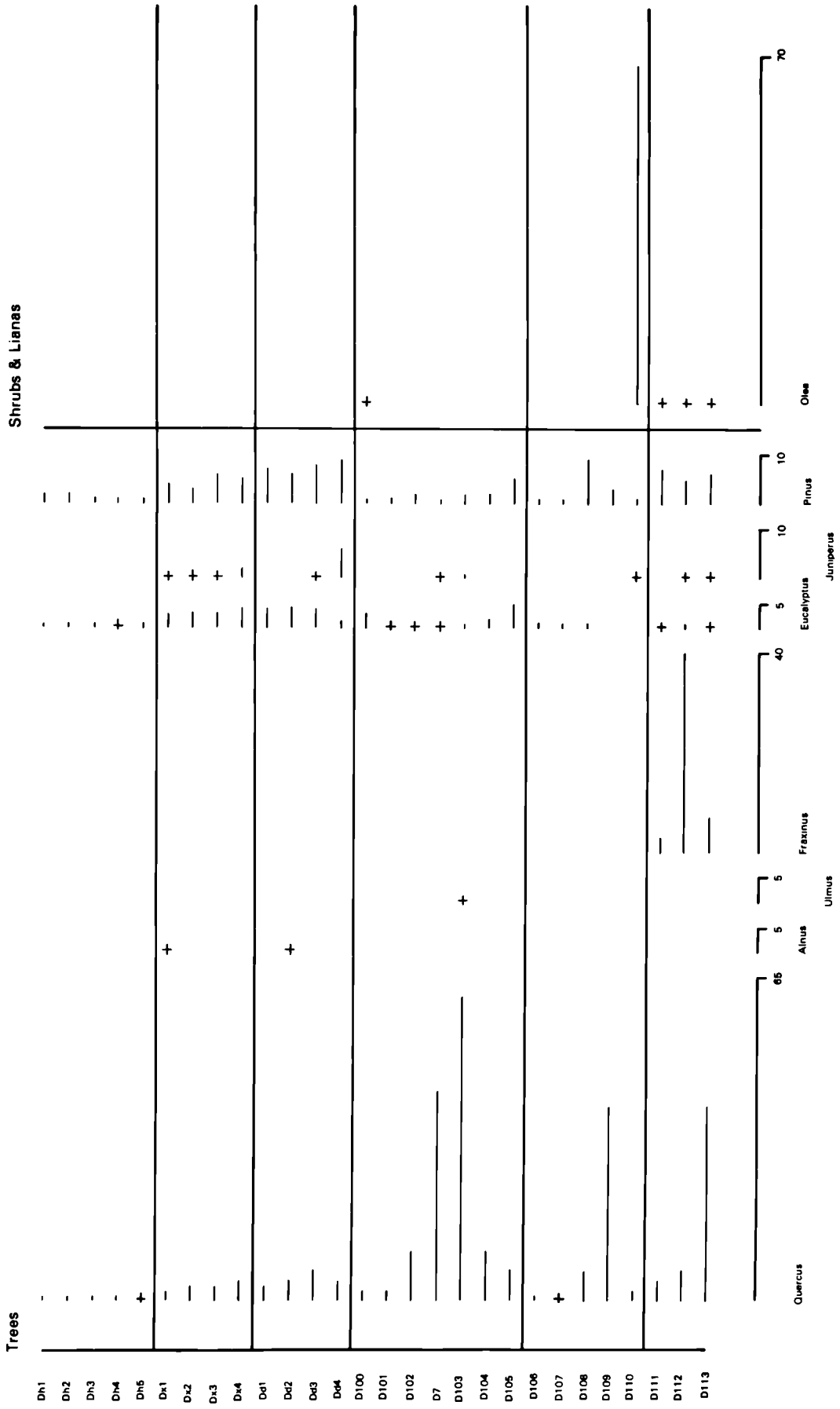

Surface Samples 1
Trees
Shrubs & Lianas
Dh1
Dh2
Dh3
Dh4
Dh5
Dx1
Dx2
Dx3
Dx4
Dd1
Dd2
Dd3
Dd4
D100
D101
D102
D7
D103
D104
D105
D106
D107
D108
D109
D110
D111
D112
D113
Quercus
65
Alnus
5
Ulmus
5
Fraxinus
40
Eucalyptus
5
Juniperus
10
Pinus
10
Olea
70

Fig.13

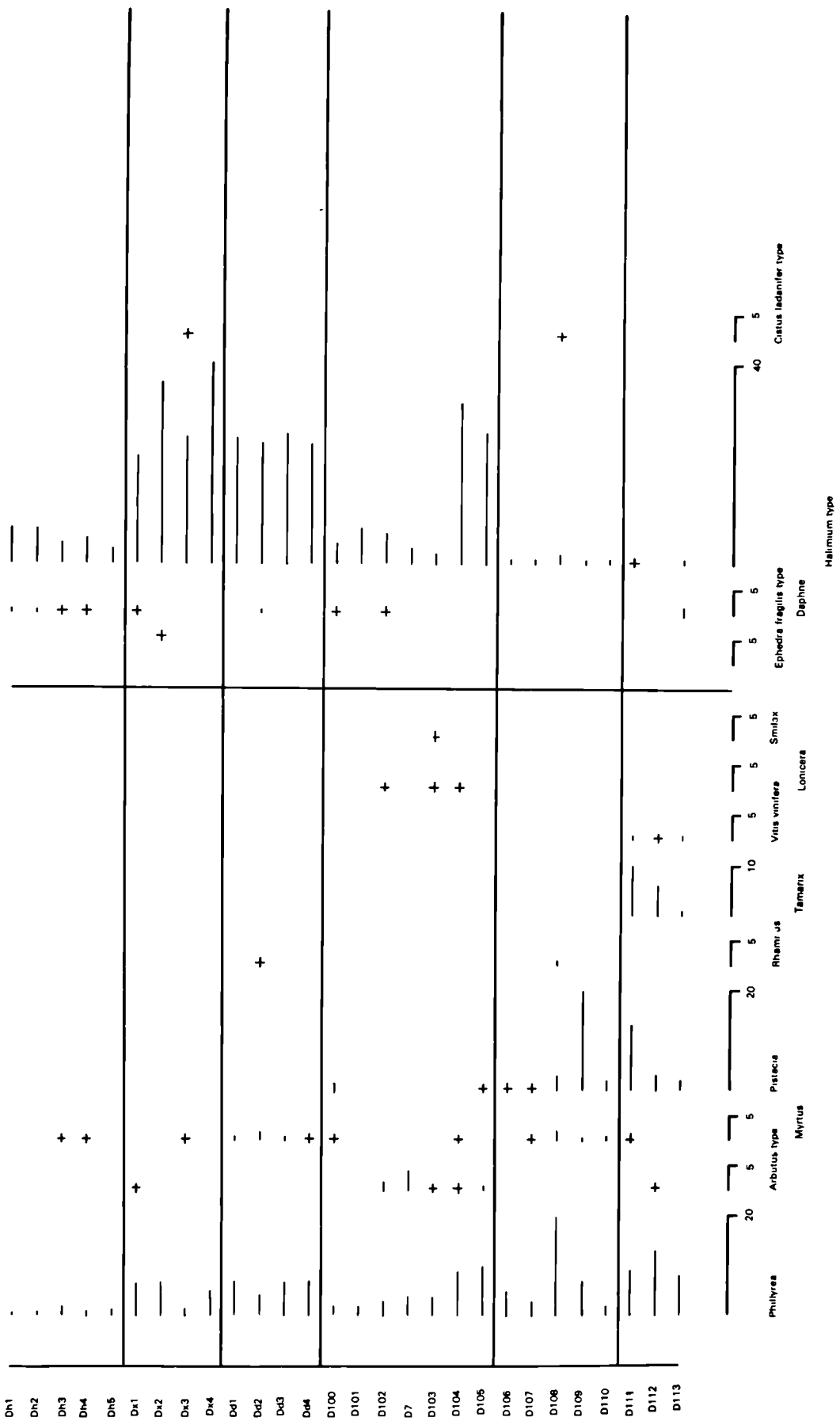

Surface Samples 1
Dwarf Shrubs
Dh1
Dh2
Dh3
Dh4
Dh5
Dx1
Dx2
Dx3
Dx4
Dd1
Dd2
Dd3
Dd4
D100
D101
D102
D7
D103
D104
D105
D106
D107
D108
D109
D110
D111
D112
D113
Phillyrea
Arbutus type
Myrtus
Pistacia
Rhamnus
Tamarix
Vitis vinifera
Lonicera
Smilax
Ephedra fragilis type
Daphne
Halimium type
Cistus ladanifer type

Fig.14

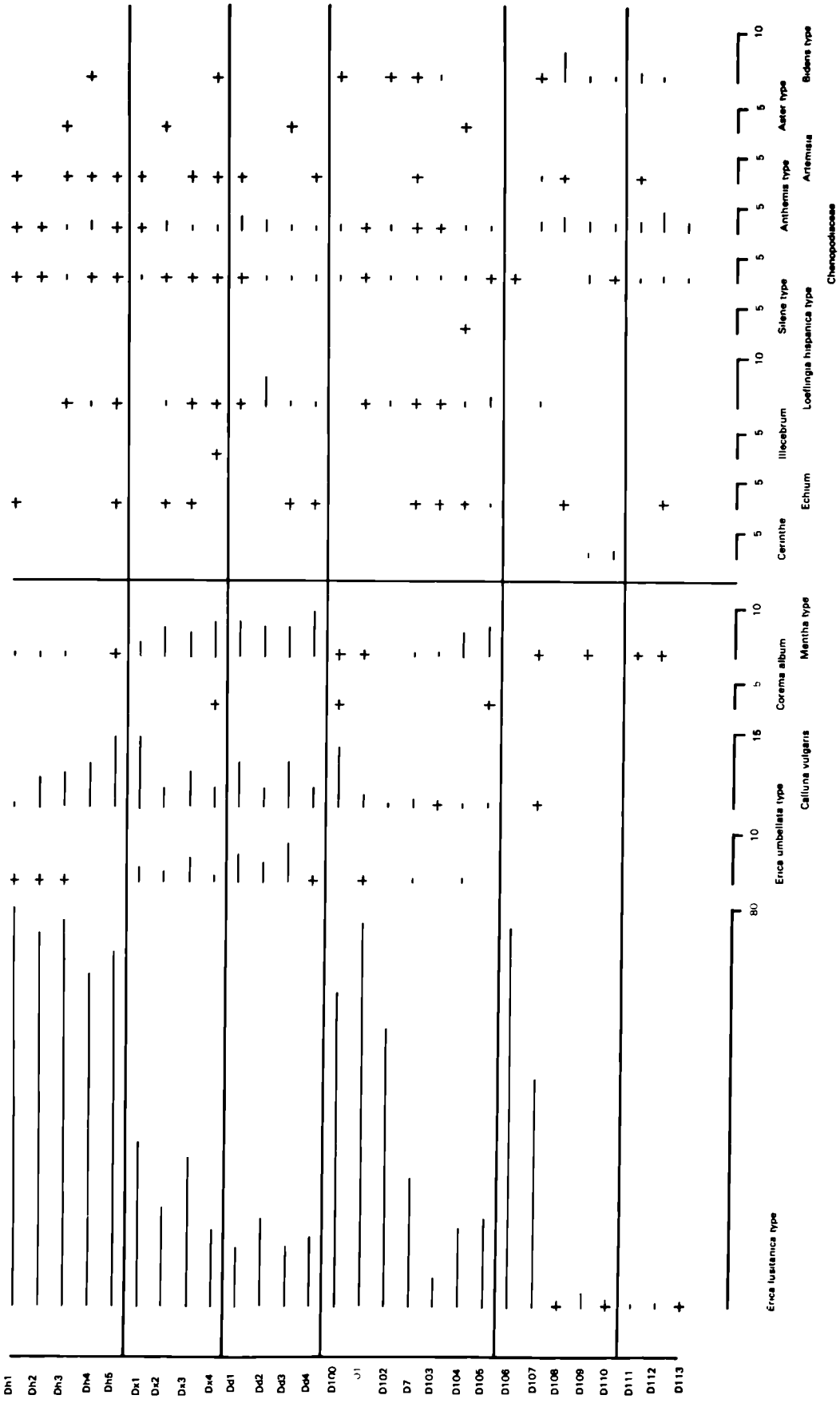

Surface Samples 1
Herbs
Dh1
Dh2
Dh3
Dh4
Dh5
Dx1
Dx2
Dx3
Dx4
Dd1
Dd2
Dd3
Dd4
D100
D102
D7
D103
D104
D105
D106
D107
D108
D109
D110
D111
D112
D113
Erica lusitanica type
Calluna vulgaris
Erica umbellata type
Mentha type
Corema album
Cerinthe
Echium
Lotus type
Lotus hispanica type
Silene type
Anthemis type
Artemisia
Aster type
Bidens type
Chenopodiaceae

Fig.15

Surface Samples 1

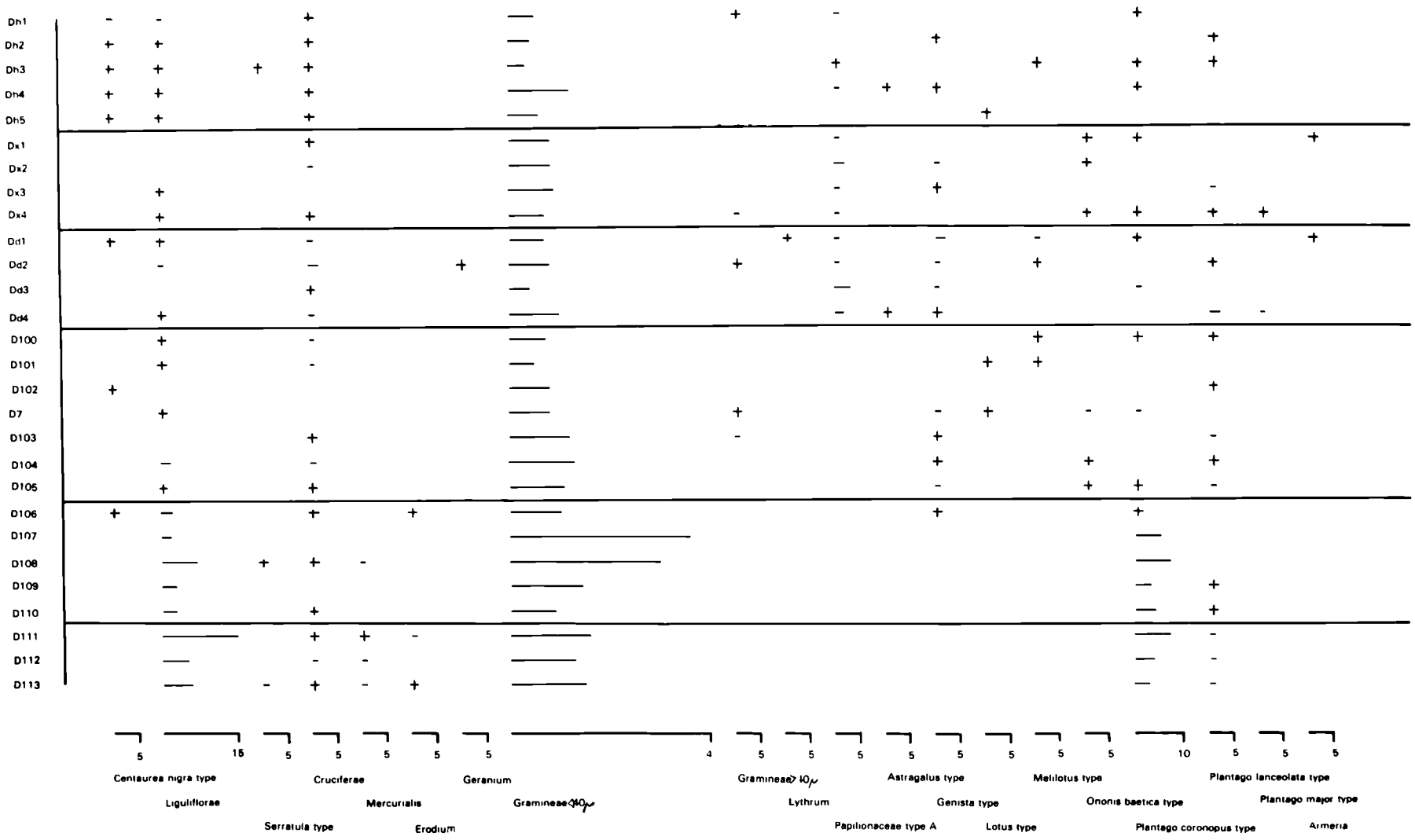


Fig. 16

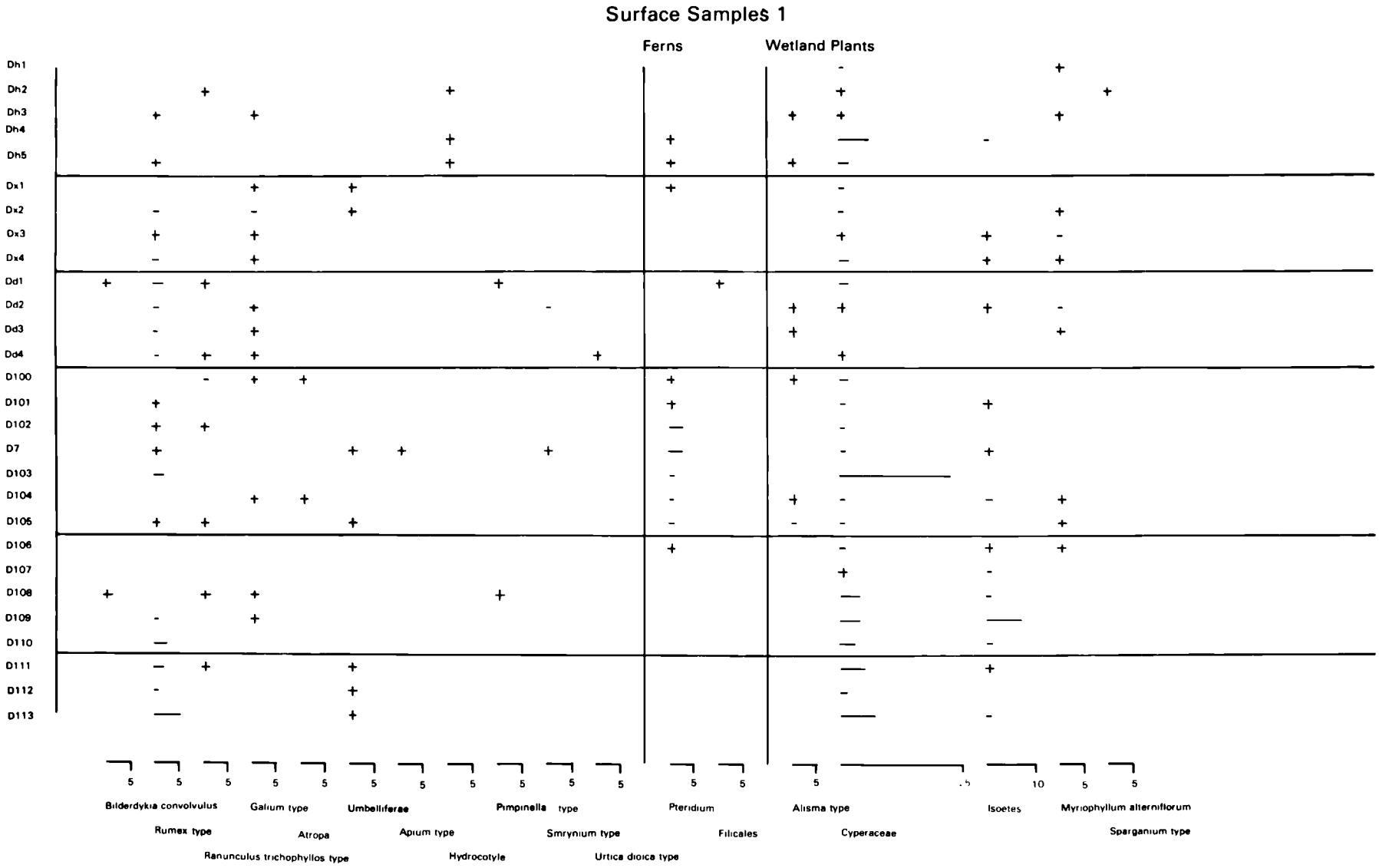

Surface Samples 1
Ferns
Wetland Plants
Dh1
Dh2
Dh3
Dh4
Dh5
Dx1
Dx2
Dx3
Dx4
Dd1
Dd2
Dd3
Dd4
D100
D101
D102
D7
D103
D104
D105
D106
D107
D108
D109
D110
D111
D112
D113
5
5
5
5
5
5
5
5
5
5
5
5
5
5
5
10
5
5
Bilderdykia convolvulus
Rumex type
Ranunculus trichophyllos type
Galium type
Atropa
Umbelliferae
Apium type
Hydrocotyle
Pimpinella type
Smrynium type
Urtica dioica type
Pteridium
Filicales
Alisma type
Cyperaceae
Isoetes
Myriophyllum alterniflorum
Sparganium type

Fig.17

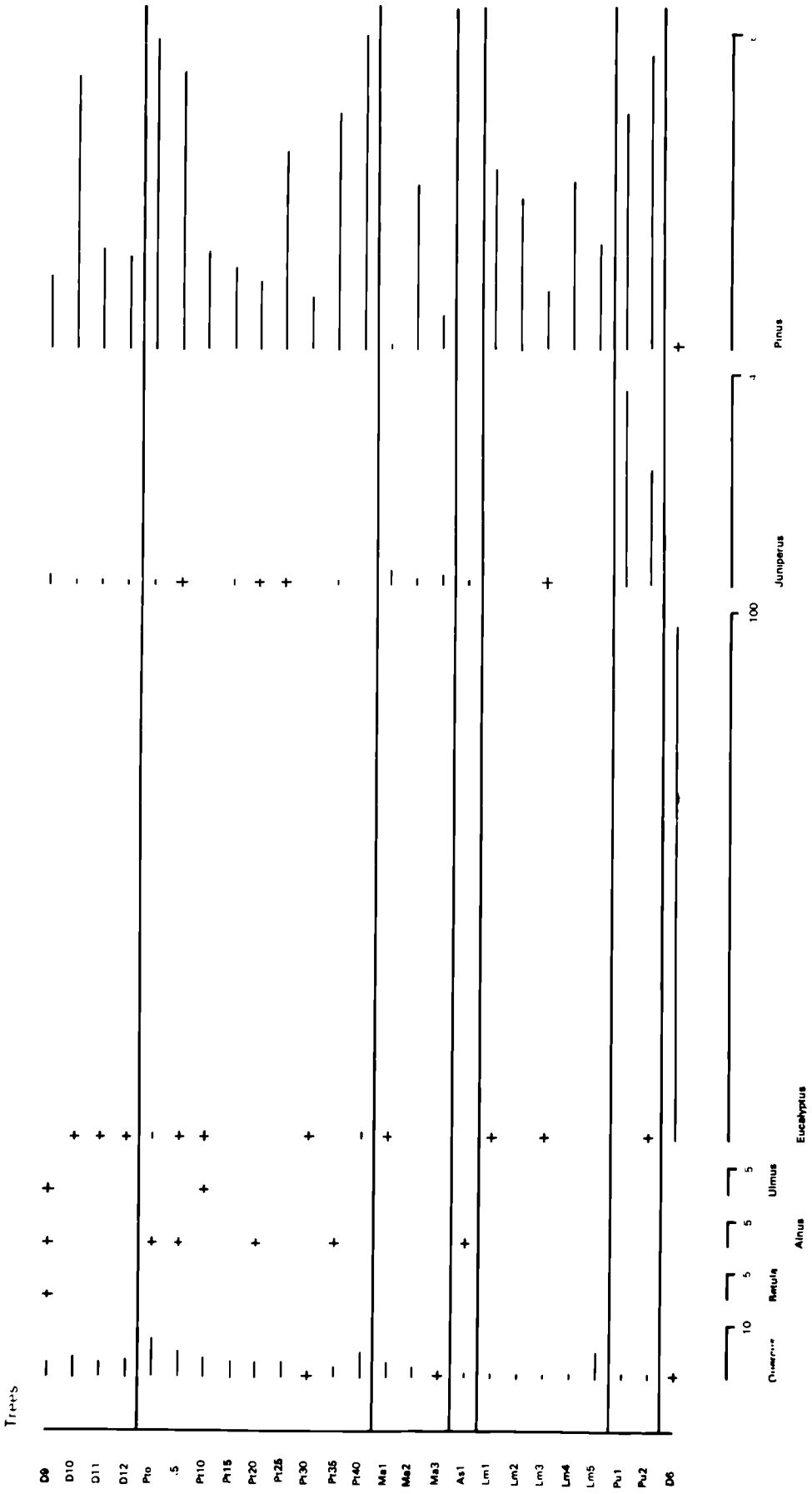

Surface Samples 2
Trees
D9
D10
D11
D12
Pto
.5
Pt10
Pt15
Pt20
Pt25
Pt30
Pt35
Pt40
Ma1
Ma2
Ma3
As1
Lm1
Lm2
Lm3
Lm4
Lm5
Pu1
Pu2
D6
10
5
5
5
100
Betula
Alnus
Ulmus
Eucalyptus
Juniperus
Pinus

Fig.18

Surface Samples 2

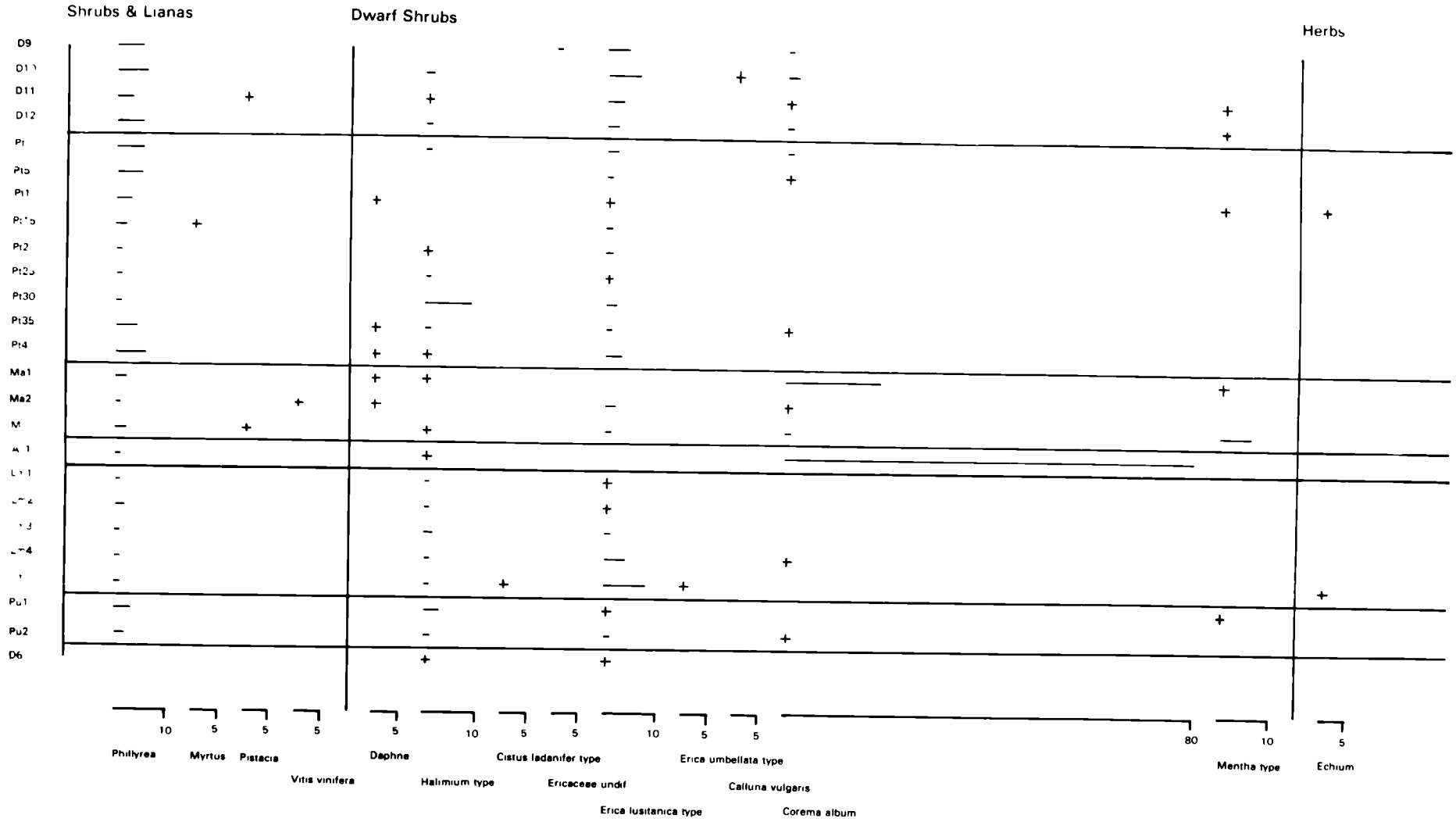


Fig.20

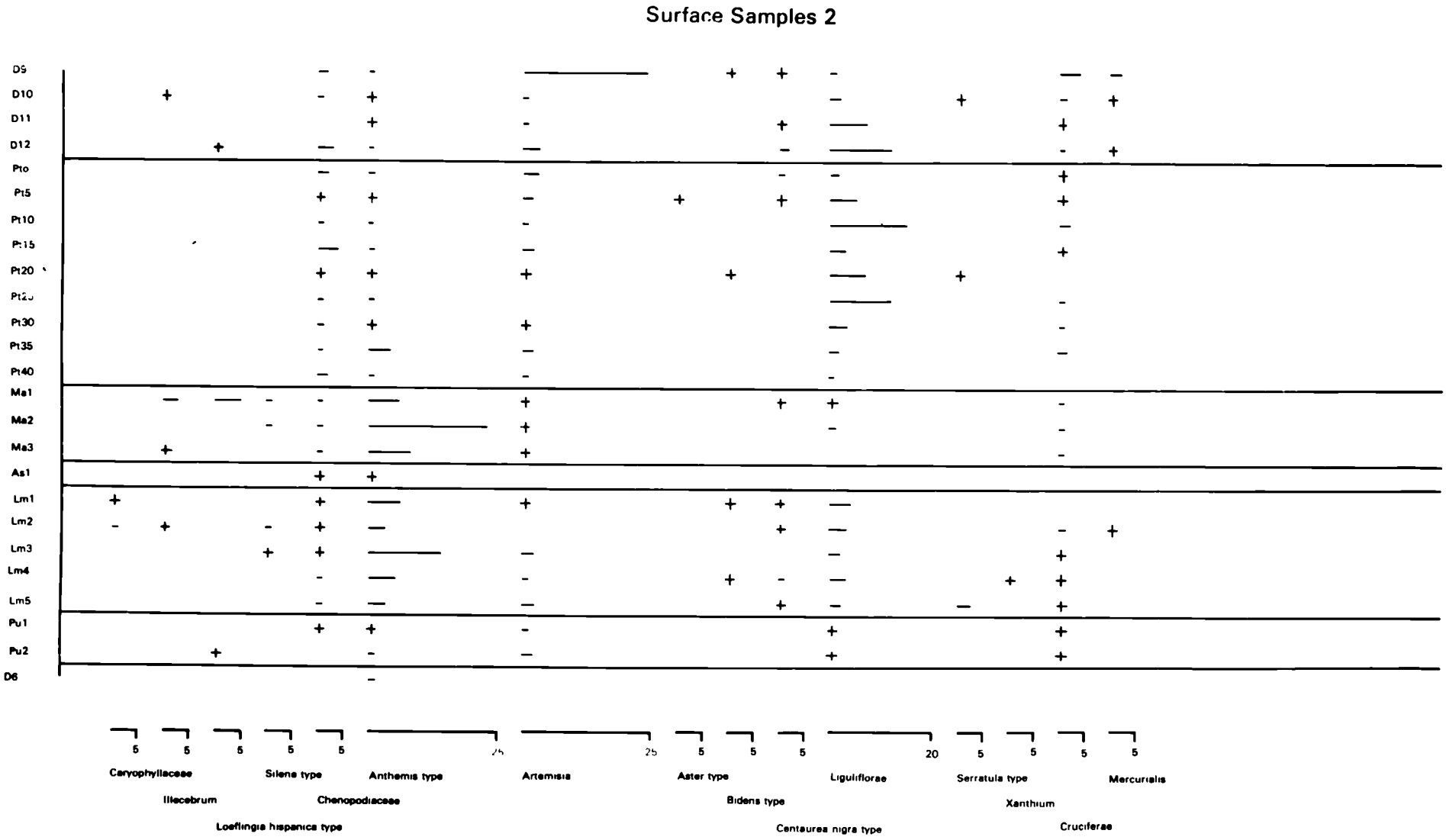

Surface Samples 2
DS
D10
D11
D12
Pto
Pt5
Pt10
Pt15
Pt20
Pt25
Pt30
Pt35
Pt40
Ma1
Ma2
Ma3
As1
Lm1
Lm2
Lm3
Lm4
Lm5
Pu1
Pu2
D6
5
5
5
5
5
25
25
5
5
5
20
5
5
5
5
Caryophyllaceae
Illecebrum
Loeflingia hispanica type
Silene type
Chenopodiaceae
Anthemis type
Artemisia
Aster type
Bidens type
Centaurea nigra type
Liguliflorae
Serratula type
Xanthium
Mercurialis
Cruciferae

Fig.19

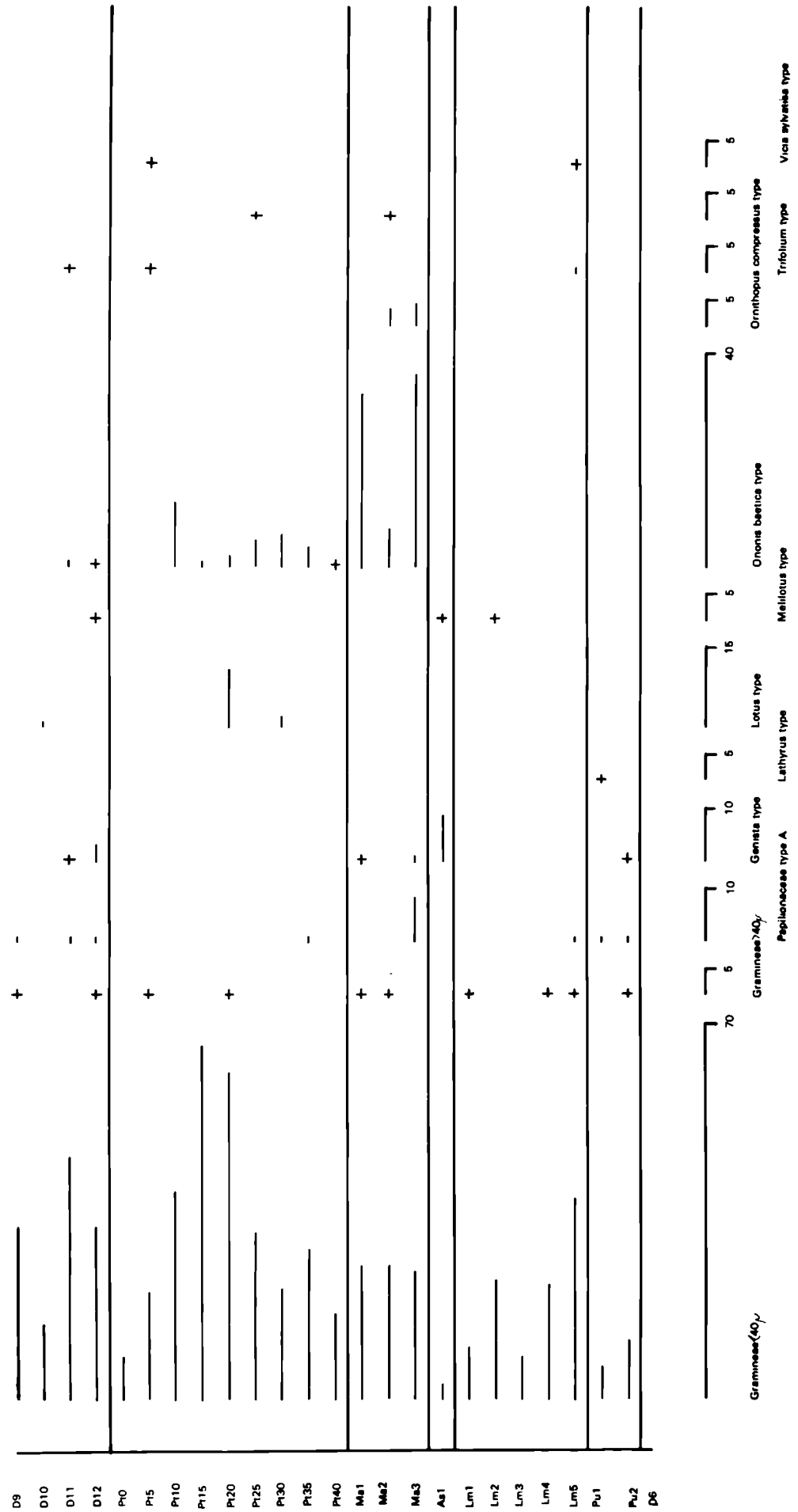

Surface Samples 2
D9
D10
D11
D12
Ph0
Ph5
Ph10
Ph15
Ph20
Ph25
Ph30
Ph35
Ph40
Ma1
Ma2
Ma3
As1
Lm1
Lm2
Lm3
Lm4
Lm5
Pu1
Pu2
p6
Gramineae(40μ
Gramineae?40μ
Papilionaceae type A
Genista type
Lathyrus type
Lotus type
Melilotus type
Ononis baetica type
Ornithopus compressus type
Trifolium type
Vicia sylvatica type
Vicia cracca type
70
5
10
10
5
15
5
40
5
5
5
5
5

Fig.21

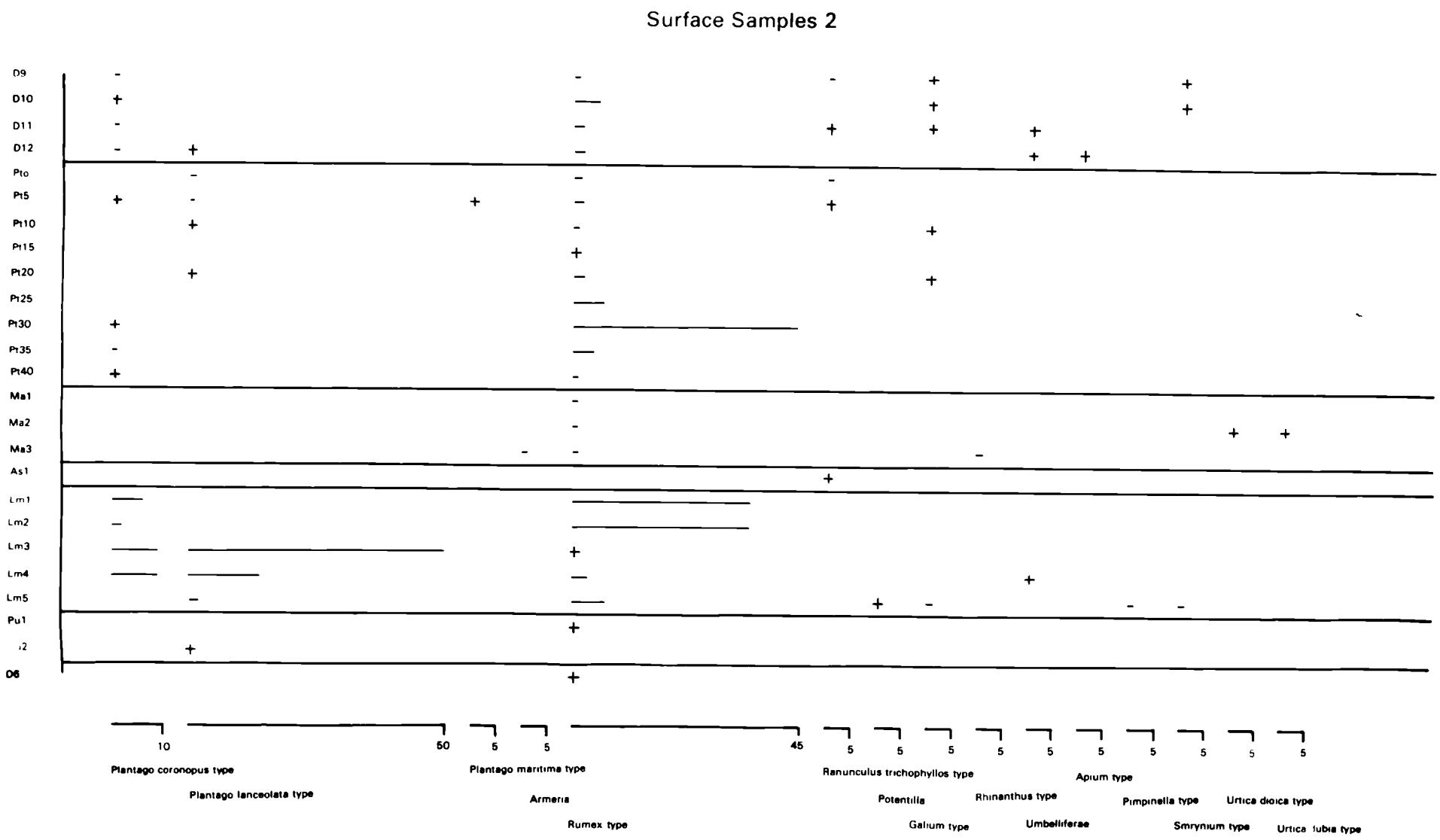
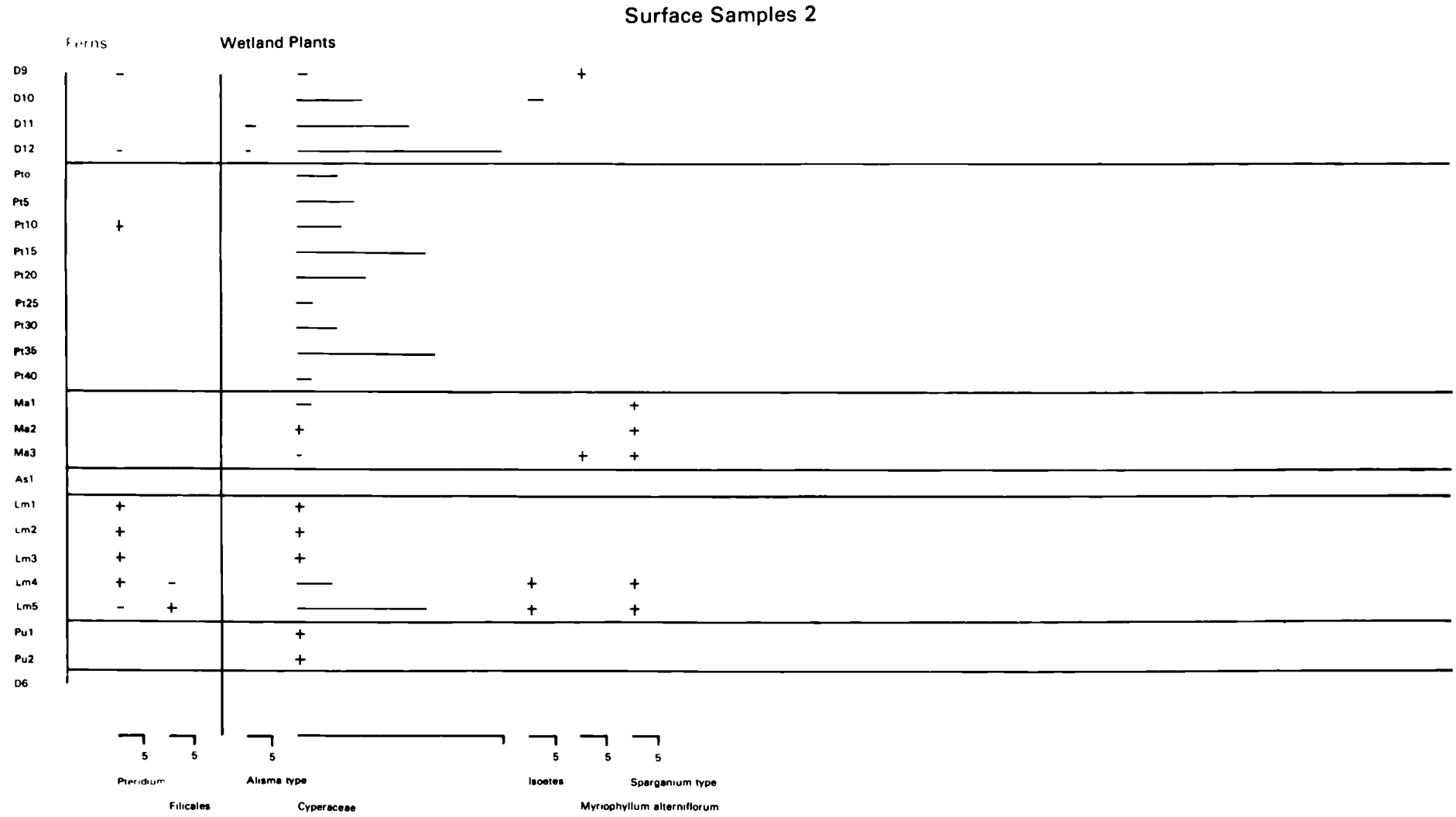

Surface Samples 2
D9
D10
D11
D12
Pto
Pt5
Pt10
Pt15
Pt20
Pt25
Pt30
Pt35
Pt40
Ma1
Ma2
Ma3
As1
Lm1
Lm2
Lm3
Lm4
Lm5
Pu1
D6
10
50
5
5
45
5
5
5
5
5
5
5
5
5
5
Plantago coronopus type
Plantago lanceolata type
Plantago maritima type
Armeria
Rumex type
Ranunculus trichophyllos type
Potentilla
Galium type
Rhinanthus type
Umbelliferae
Apium type
Pimpinella type
Smrynium type
Urtica dioica type
Urtica lubis type

Fig.22


Surface Samples 2
Ferns
Wetland Plants
D9
D10
D11
D12
Pt0
Pt5
Pt10
Pt15
Pt20
Pt25
Pt30
Pt35
Pt40
Ma1
Ma2
Ma3
As1
Lm1
Lm2
Lm3
Lm4
Lm5
Pu1
Pu2
D6
5
5
5
5
5
5
Pteridium
Filicales
Alisma type
Cyperaceae
Isoetes
Sparganium type
Myriophyllum alterniflorum

Modern Pollen Survey Discussion

1) Monte blanco shrub communities

The pollen rain of this community is characterised by high Halimium type values, high Mentha type (5%) and low Erica lusitanica type. The plants responsible for high Halimium type are Cistus libanotis, Halimium commutatum and H. halimifolium, and in previous studies of Cistaceae dominated communities it has been found that they tend to be seriously under-represented, e.g. studies by Bottema and Barkoudah (1979). In Syria and Lebanon in sites containing Cistus salvifolius they found Cistaceae representations of 0.8% and this was also found to be true of studies by Van Zeist et al (1975) working in S.W. Turkey. Although it is now possible to differentiate the Halimium spp. from the Cistus spp. (see Appendix A), the separation was not performed in the present study due to lack of type material. Thus the Halimium type includes all Halimium spp. and Cistus spp. except for C. ladanifer pollen type. Sites D107 and D109 both have Cistus salvifolius present and the representation of the pollen is low, confirming the under-representation noticed in the previous studies, and even in sites that contain Halimium spp., such as D112, Mal-3 values of Halimium type pollen remain low. The reason why the pollen representation of Halimium is high in the shrub communities (Dd1-4 and Dx1-4) may be the larger populations of Halimium and Cistus spp. found in these communities than in sites such as D112 and Mal-3. Thus higher densities of plants may be necessary before pollen values start to reach high values, e.g. in sites D113, Ma1, As1, Pu1, Pu2, where members of the Cistaceae were present but in low numbers, 1,6,1,1,1 respec-

tively, the values of Halimium type pollen recovered were also low. (N.B. 6 plants would approximate to a value of 1 on the Braun-Blanquet scale used to assess the other populations) while in the Dd, Dx, D104 and D105 sites the numbers of Cistaceae present reach a total cover of 5 on the Braun-Blanquet scale,which represents total dominance, and it is only here that the values of Halimium type pollen become high, i.e. 20-30% of the total pollen. This feature of the effect of density on pollen representation will be seen to be repeated for Juniperus. The Mentha type pollen largely derives from Rosmarinus officianalis and Lavandula stoechas. However, considering that these two species are common in the community the pollen values are not as high as would be expected and thus these two species are under-represented in the pollen rain. The low Erica lusitanica pollen input reflects especially the absence of Erica scoparia from the monte blanco shrub community.

Other species that are under-represented in the pollen rain are Genista anglica, Helichrysum italicum and Juniperus phoenicia. Under-representation of Genista anglica is to be expected because of its insect pollination. In many studies e.g. Bottema and Barkoudah (1979) pollen of the Leguminosae in general is found to be seriously under-represented in the pollen rain, which is a feature that will recur throughout this study. Helichrysum may have been expected to be well represented in the pollen rain despite it being insect pollinated for it has been found in many surface studies of the Compositae that the input into the pollen rain can be high (Cf Liguliflorae) in the Iranian sites. In site Dd4 one tree of Juniperus phoenicia was observed to be growing but it was hardly represented in the pollen rain of the site (0.4%). This feature of the pollen rain of Juniperus will be discussed later in connection with the monte blanco forest communities.

Other species that are under-represented are Leucojum sp. and Loeflingia baetica. The representation of Loeflingia is variable, however, and there is an indication of strong representation at site Dd2, which may indicate very local deposition of pollen. It is noticeable that large quantities of Loeflingia pollen were recovered from the core at Encinillas Altas (Chapter 5).

A feature about the pollen rain of these monte blanco shrub sites is the non-local component of pollen input into the site. Already mentioned has been Erica lusitanica type: other types characteristic of the long distance component are Pinus, Phillyrea, Erica umbellata, Calluna, Rhamnus and Myrtus. All these species occur in the surrounding mosaic of vegetation on monte negro and monte negro hygrophytic sites and there seems to be a tendency for the last five of these types to be exported from the monte negro hygrophytic sites where they occur. This feature of exportation from the site of production has been noted before in the case of Calluna vulgaris in Britain (P.D. Moore personal communication). A more detailed discussion about the pollen representation of Pinus pinea is to be found later on. Other pollen types whose input must derive from greater distances than those just seen also occur, e.g. Quercus pollen, the nearest tree being 4km away, Eucalyptus pollen, the nearest tree being 5km away and Alnus, a species absent from the area.

There are probably two reasons why these monte blanco sites have a large amount of non-local derived pollen input, especially when compared with the monte negro hygrophytic

sites:-

i) Pollen production of the monte blanco is lower than that of the monte negro hygrophytic communities.

ii) Openness of the structure of the vegetation of the monte blanco when compared with the monte negro hygrophytic. Thus the filtering effect that Erica scoparia would have in the monte negro hygrophytic is absent from the monte blanco.

In tundra and desert regions of the world it is often found that a high amount of non-local pollen is recovered from samples. It is thought that this is due to the poor pollen productivity of the plants that inhabit such areas (Ritchie and Lichti-Federovich, 1967). While this may be part of the cause of the high representation of non-local pollen in the monte blanco sites, one must not underrate the effect of the filtering component of dense vegetation as is to be found in the monte negro hygrophytic sites.

The level of Gramineae pollen is also low when compared to arid sites from America (Schoenwetter 1971), this can be explained by the absence of arid adapted grasses in this part of the reserve. The Cruciferae input is probably derived from plants of Malcomia littorea, a plant that colonises bare patches of sand in the same mode as Loeflingia baetica.

2) Monte negro shrub communities

The pollen rain of this community is very similar to that of monte blanco shrub communities despite having a greater

variety of plants present that may assume dominance in the community. The community is dominated by large numbers of Leguminosae:- Stauracanthus genistioides, Genista anglica, Ulex minor and Spartium junceum. Despite this large component of Leguminosae plants, very little Genista type pollen is found in the pollen rain, and thus confirming the considerable under-representation of the Leguminosae in general (Van Zeist et al 1975), (Iran Part A). Thus when interpreting fossil pollen diagrams this fact must be borne in mind. Other plants typically under-represented, despite growing in the quadrats, are Osyris quadripartita, a parasite on Halimium sp. (a feature found before by Bottema and Barkoudah (1979)), and Fritallaria lusitanica in site Dx4.

The increased proportion of Erica lusitanica type pollen is probably due to the occasional presence of bushes of E.scoparia which do not achieve the densities seen in the monte negro hygrophytic shrub.

Once again the non-local pollen rain of this site is high (5%) and is comparable to that just seen in the monte blanco shrub communities. The reasons postulated for this input in the monte blanco hold here for the monte negro shrub systems which are again open structured system when compared with the monte negro hygrophytic shrub.

Another pollen type that has been transported long distances is that of Ephedra fragilis type. Ephedra today in Spain is restricted to high arid mountainous regions, with the nearest source being the Sierra Nevada. Such transport has been

found to be characteristic of Ephedra pollen (Maher 1964, Vinje and Vinje 1955). This feature of Ephedra pollen rain will be discussed more fully in relation to the fossil pollen site at El Asperillo.

The presence of Illecebrum pollen also must represent pollen movement from outside of the sample area since Illecebrum is not recorded from the vegetational survey, and that the plant is characteristic of wet grassland communities derived by grazing of the monte negro hygrophytic communities.

The occurrence of Cistus ladanifer type pollen, which includes four members of the Cistaceae in Spain - C. populifolius, C. monspeliensis, C, laurifolius and C. ladanifer, probably comes from plants of Cistus ladanifer, which invaded the reserve when a new road was built with material from outside of the reserve, which was more acidic and contained more potassium than is found in the soils of the reserve.

3) Monte negro hygrophytic shrub communities

The pollen rain of this community in contrast to that of the previous two is dominated by Erica lusitanica type pollen, reflecting the dominance of Erica scoparia in the community. Halimium type and Mentha type frequencies are low, reflecting their scarcity or absence from this community, although Cistus salvifolius is found in all of the sites.

The non-local component of the site, chiefly Quercus and Eucalyptus is very low when compared with the previous two

sites. The reasons for this have already been mentioned in connection with them, i.e. that the monte negro hygrophytic shrub community may have a greater pollen productivity and a greater filtration effect on any imported pollen.

Values of Pinus are also low, this may be due to the aforementioned effects of pollen productivity and filtration, but site Dh2 had a large tree of Pinus present in the sample area and the tree is planted throughout the area. Since it is normally felt that Pinus is heavily over-represented in many plant communities (Anderson 1970), the low values of Pinus are all the more surprising. Two possible causes for these could be:-

i) Pinus grows well above the canopy layer of the shrubs, e.g. Erica scoparia, and because the shrub canopy is so dense, this may provide the filtration of Pinus pollen input needed to reduce the values or more probably that Erica scoparia is so heavily over-represented that the values of Pinus are reduced. However, it is noticeable that even in the more open communities, Pinus pollen values do not go above 7% Therefore:-

ii)The possibility that Pinus pinea may be a poor pollen producer and its pollen poorly dispersed must be examined. (This point is discussed further on p. 118.

The over-representation of Erica scoparia is very noticeable in site Dh4 where, although dominated by Agrostis stolonifera, the values of the Gramineae only reach 10%, about double that

which is normally found in these sites. The large amount of Eleocharis palustris also present, also does not give rise to a strong increase in the Cyperaceae records for the site. Very little previous work has been conducted into the pollen productivity of Erica sp. but in general it has been found that they do tend to be well represented in the pollen rain, e.g. Erica verticillata in S.W. Turkey (Van Zeist et al 1975) produced 12.5% of the pollen rain in vegetation dominated by Pinus brutia which was found to dominate the pollen rain, (74%) Cf. site Dh2.

Daphne pollen is constant throughout, but is under-represented throughout the humid sites.

Many plants present in the monte negro hygrophytic communities are under-represented and once again this is a feature of members of the Leguminosae, this time Ulex minor and Cytisus grandiflorus. Under-representation is also a feature of the following species -: Rubus ulmifolius (frequent as an understorey in Erica scoparia), Anagallis arvensis, Juncus sp., Hydrocotyle vulgaris, Hypericum sp. (all species from grazing derived grassland Dh4), Myrtus communis, Cistus ladanifer. Under-representation of Myrtus has been found to be characteristic of many communities in which it is found and contrasts with the over-representation seen by Eucalyptus a member of the same family.

4) Monte blanco forest communities

i) Juniperus dominated communities, Pu1, Pu2

These two sites were dominated by Juniperus phoenicia

and J. oxycedrus, of which J. oxycedrus is thought to be the more oceanic of the pair (G. Novo 1979). This system is the endpoint of succession from a monte blanco shrub community under stable conditions and has a Juniperus pollen rain of 37% in Pul and 22% in Pu2. However, considering that Juniperus dominated the flora of the sample quadrat, the representation of Juniperus in the pollen rain is low, Pinus provides a large component of the pollen rain even though it is not present in the quadrat. However, the values of Juniperus pollen recorded here are high when compared with many other surface sample studies of Juniperus communities. Even in the present study Juniperus pollen representation is very variable. Site Mal, Ma2, and Ddl illustrate this point, with low Juniperus pollen even though trees of Juniperus are present in the sample quadrat. This variability of the pollen rain was also found by Van Zeist et al (1975) working in S.W. Turkey, where they found values from sites dominated by J.oxycedrus from 3.3% - 19.3% and in a sample site dominated by J. excelsa it reached 23.7%. Surface sample studies from the Alps by Beaulieu (1977) revealed that the pollen rain of J. thurifera communities was also low, the highest being 7%. The variability of Juniperus pollen representation was also found to be repeated in studies of J. communis communities from the Isle of Skye. It is noticeable that in the present studies the highest values of Juniperus representation in the pollen rain came from those communities dominated by a large number of Juniperus trees such as Pul and Pu2. Sites with low amounts of Juniperus pollen were ones that only had one

or two trees and the system was relatively open, e.g. sites Dd1, Ma1, Ma2. Thus the density of Juniperus trees seems to have an effect on Juniperus representation in the pollen rain. This feature of the effect of the structure and density of Juniperus on the pollen rain was also found in the study of the J. communis communities on the Isle of Skye by Birks (1973). Thus the partial answer to the variability of Juniperus pollen rain appears to have been found. Undoubtedly though Juniperus is still under-represented even when the pollen values reach 37%.

The under-representation of leguminous plants is repeated here e.g. Ornithopus compressus, Medicago sp. Under-representation is also noticeable of Rhamnus lycioides, Linaria sp., Thapsia villosus and Centranthus sp.

ii) Pistacia/Phillyrea communities

In these forests derived from the monte blanco shrub communities under stable conditions and on the more silty soils, occur communities dominated by Pistacia lentiscus, with Phillyrea angustifolia as a common associate, often in the centre of the Pistacia bush, presumably offering a more humid microclimate than outside it. The pollen rain from these communities provides some interesting comparisons with the work conducted in N.E. Iran and from many other Pistacia dominated communities from the Eastern Mediterranean and Near East.

In the sites sampled for the present study, the pollen rain of Pistacia was found to be very variable, just as with that of Juniperus. In sites D106 and D107 the values of Pistacia were very low despite at least one large bush in each site. The pollen rain of these two communities was dominated by Erica lusitanica type, a type that has been shown to be seriously over-represented, but even if this type is removed from the pollen sum the values of Pistacia still remain very low, which points to distinct under-representation of Pistacia. This is all the more surprising for Pistacia is a wind pollinated plant. Similar results were found in studies of a Pistacia forest from N.W. Iran (Wright et al 1967) where the highest value recorded was 4.5% of the pollen rain. Results from N.E. Iran (this thesis) also bear this feature as do the studies of Bottema and Barkoudah (1979) in Syria and Lebanon, Van Zeist et al in S.W. Turkey (1975), Beaulieu (1977) of P. terebinthus communities in France. Even site D108, again dominated by a large Pistacia bush and without the influence of Erica scoparia in D106 and D107, only managed to produce 3.3% Pistacia pollen. The highest value of a Pistacia community so far has been the work of Van Zeist et al (1975) in S.W. Turkey where a value of 8.1% was obtained, which is still very low, pointing to serious under-representation. However, in the present study two sites produce comparatively high representations of Pistacia pollen, these being D109 with a value of 20% (despite a large proportion of Quercus and Erica lusitanica type pollen present) and

D111 where the Pistacia representation was 13.3% but no bush was recorded from the sample quadrat (a bush however was observed nearby). This variable feature of the pollen rain of Pistacia communities has puzzled many workers. The results must however, be interpreted in the knowledge that the genus is dioecious. It is known for certain that the Pistacia bushes in sites D106, D107 and D108 were female. The bush in D109 was definitely male for pollen samples were obtained from it. Thus this feature of reproduction of Pistacia may explain the low representation found by many workers. Therefore the representation of Pistacia in the pollen rain will depend on the proportion of male Pistacia bushes in the population.

The pollen rain of Phillyrea also follows a similar variable pattern to that just seen in Juniperus and Pistacia. The pollen values vary from 2.9% in site D107 to 20% in D108. The values in D106 and D107 may have been affected by the over-representation of Erica lusitanica type pollen, but even on exclusion from the sum the percentages still remain low. Low values of Phillyrea have been found before in this study, most notably in the monte negro hygrophytic shrub sites, but here Erica lusitanica type pollen is again over-represented. It has also been observed that considerable movement of pollen takes place from these monte negro hygrophytic sites, higher values being recorded from the adjacent monte negro and monte blanco sites (Cf.Dh, Dx, Dd, D100-D105). Phillyrea angustifolia has also

been found to be under-represented in studies by Van Zeist *et al* (1975) in S.W. Turkey. Thus in general *Phillyrea* is seriously under-represented in sites where it occurs, but manages to be efficient disperser of its pollen.

The *Plantago* type, *Anthemis* type, *Bidens* type and *Liguliflorae* values are all higher compared to the shrub communities from which this system has developed. This is a feature of the Park-like nature of the system, with large areas of open ground, subject to disturbance, compared to the shrub system.

The one plant of *Rhamnus lycioides* recorded from site D108 only gave rise to 0.8% representation in the pollen rain, thus confirming the tendency already noticed for pollen of the Rhamnaceae to be seriously under-represented (Van Zeist *et al* 1968 in S.E. Turkey, and Bottema and Barkoudah 1979 working in Syria and Lebanon). Other plants that are noticeably under-represented are *Bryonia cretica*, *Ruscus aculeatus*, *Pyrus bourgeana*, *Asphodelus cerasifer*, *Smilax aspera*. *Asphodelus* and *Smilax* have also been found to be seriously under-represented in the studies in Syria and Lebanon by Bottema and Barkoudah (1979). The pollen of *Myrtus communis* behaves very similarly to that of *Phillyrea* in that it is a poor pollen producer (D106 and D107) but is an efficient disperser of pollen, e.g. site D108.

7.4% of *Isoetes* pollen was recovered from site D109,

this would indicate that local winter flooding of the site is occurring. The site in many respects is intermediate between that of monte blanco forests and monte negro forests: the high silt content of these soils in the north of the Park could lead to increased occurrence of winter flooding compared to the more freely draining sandy soils in the south of the Park.

5) Monte negro forest communities

Only one sample was taken from this community (D110), but an interesting feature of the pollen rain is the high representation of Olea (68%), from just one tree of Olea europaea in the quadrat. This is despite the presence of a large tree of Pinus pinea present just outside the quadrat, which points to Pinus pinea not being a high pollen producer when compared to many other Pinus sp. High values of Olea pollen have been found to occur in previous studies in Greece (Bottema 1974) and in S.W. Turkey (Van Zeist et al 1975). Both of these studies and also studies of Reille (1975) and Beaulieu (1977) have found Olea to be very well dispersed. However, this does not seem to be true of the present study, where sites D108 and D109, the nearest to D110 produce no Olea pollen, a feature confirmed by Bottema and Barkoudah (1979). Thus Olea appears to behave differently from its close relative Phillyrea in that Phillyrea is a poor pollen producer but is an efficient disperser of pollen.

Again Pistacia is seen to be under-represented, the possibility is that these were female plants but this feature could not be recorded at the time of sampling, due to the absence of any

inflorescences. Another species that is under-represented is Chamaerops humilis, the only native palm species of Europe, a feature which is repeated in the transect at Laguna de las Madres. The cause of the under-representation again is related to the reproductive mode of the plant, for this plant too is dioecious. The sex of the plants in the quadrat could not however, be ascertained due to absence of inflorescences. Characteristic under-representation is also seen in Stauracanthus genistioides, Daphne gnidium, Cistus salvifolius, Rhamnus lycioides and Halimium halimifolium. The low value of Halimium type being a reflection of the low density of Halimium sp. present and the over-representation of Olea.

6) Monte negro hygrophytic forest communities

The pollen rain of this community is very variable. Sites D101 and D102, although trees of Quercus suber were present in the quadrat, contain very little pollen of Quercus, i.e. 2% and 15% compared to sites D103 and D7 where values are high, 62% and 42% respectively. The difference in the two sets of values reflect the position of the sites in relation to the surrounding vegetation. D101 and D102 were both from outside the dense canopy being formed by the Q. suber trees in D103 and D7, and the ground flora outside the dense canopy was dominated by Erica scoparia and other plants typical of monte negro hygrophytic shrub vegetation. As we have seen before Erica scoparia is seriously over-represented in the pollen rain and thus reduces the values of Quercus. This is further confirmed by evidence from sites D109 and D113 where high Quercus values were recorded although only single trees were present, and since these samples were from sites where

the vegetation was not dominated by any plants that are over-represented. Samples from D103 and D7 were also from sites where Erica scoparia was absent and thus the values reflect the dominant position that Quercus holds in the community.

A plant that is considerably under-represented is Smilax aspera despite forming dense impenetrable thickets through most of the Quercus suber forest. Only two grains were recovered (D103) despite Smilax being present throughout the samples D101-103. This feature was seen to occur in the monte blanco forest sites (p.112). Arbutus unedo, a tree that forms an understorey in the Quercus forest also is seriously under-represented in the pollen rain. Sites D101 and D103 that contain the tree only produce at a maximum 1.8% in the pollen rain, and previous studies by Van Zeist et al (1975) in S.W. Turkey have also confirmed this feature. Pteridium too is also under-represented despite it forming the major ground cover in the more open parts of the Quercus forest.

The values of Phillyrea are again low (in the range 2-10%) in sites D100-103 but the efficient dispersal of Phillyrea is again shown by the high inputs into the monte negro sites outside the Quercus canopy (D104 and D105, but also see p.117).

Of additional interest are the two grains of Atropa that were observed in D100 and D104. The species has not been recorded from the Park thus the origin of these grains must represent long distance transport. This also applies to the grain of Ulmus recovered from D103, which has also been found in other

sites, e.g. D9 and Pt10, since Ulmus is not recorded from this part of Spain.

The set of samples D100-D105 represent a transect every 20m from a monte negro hygrophytic shrub community into the derived forest community dominated by Quercus suber and out into a community dominated by monte negro shrub vegetation. The pollen rain of the two shrub communities are very similar to those described on pgs.103 -107 . The high input of non-local pollen into the monte negro hygrophytic shrub community, a feature not found in the previous study of such communities, is due to a fire that had recently occurred and had opened up the monte negro hygrophytic shrub community thus removing the potential high filtration of pollen by Erica scoparia.

The rapid decline of Quercus pollen on emerging from the canopy is very marked, an effect which has been seen to occur in many studies (Smith and Tinsley 1974). Quercus values also fall more quickly as one moves into the monte negro hygrophytic shrub community, due to the high over-representation of Erica scoparia compared to the monte negro communities, where the fall is less sharp but is still marked.

The values for Pinus rise along the monte negro transect D104-D105, this is due to the line approaching a plantation of Pinus pinea. The Phillyrea values again show that much of the pollen production seems to be exported from the site of production. However, one would think that the dense cover of Smilax in the forest would hinder trunk space pollen flow (Tauber 1965), which is where Phillyrea would undoubtedly

discharge its pollen. The high values of Phillyrea may however, not have their origin in the Quercus forest, but from the surrounding monte negro hygrophytic shrub communities containing Phillyrea. In these communities Phillyrea becomes effectively part of the canopy and thus discharges its pollen into a canopy component of pollen rain, which is well represented in the surrounding monte blanco/negro shrub types where the over-representation of Erica scoparia is not apparent, which keeps the values of Phillyrea pollen in the monte negro hygrophytic communities very low.

7) Fraxinus/Tamarix communities

Despite Fraxinus being a dominant tree in each of the three sites examined, its contribution to the pollen rain was very variable, with only 3.4% in D111 to 6.6% in D113, with a maximum of 40% in D112. Thus in general Fraxinus angustifolia appears to be under-represented, which was a feature of the pollen rain of Fraxinus communities from S.W. Turkey (Van Zeist et al 1975)

Tamarix africana which was a major constituent of the understorey of these Fraxinus dominated sites, is also seriously under-represented in the pollen rain, and again was a feature of its pollen rain that has been found in many studies, e.g. N.E. Iran (this thesis) and (Van Zeist et al 1968) in S.E. Turkey where values only reached 0.3% from within a dense stand of Tamarix. The current values of Tamarix pollen do not go as low as these results but the shrub is still under-represented when the cover of the shrub is considered.

Due to the high amount of bare soil in these sites the values

for Anthemis types, Bidens type, Liguliflorae and Plantago type are all high in comparison with the shrub systems already examined. The openness of the system and the low pollen productivity of the major components of the vegetation lead to a high input of non-local pollen, e.g. Pinus and Eucalyptus. Phillyrea values are very high considering that the tree was not recorded from the sample quadrats. Thus, once again Phillyrea is shown to be an efficient disperser of pollen.

A major point is the presence of Vitis vinifera growing as a liana on Fraxinus angustifolia in site D113. As can be seen, its contribution to the pollen rain is very low, 0.8%, a similar situation was also found in studies on natural Vitis populations in Syria and Lebanon by Bottema and Barkoudah (1979), Van Zeist et al (1968) and (1975) in S.E. and S.W.. Turkey respectively. Thus under-representation of natural Vitis populations is very characteristic. It is interesting to note that the same kind of values were obtained from Hoxnian sites in Britain (Marks Tey, Turner 1970) and this evidence would point to Vitis occurring as a natural component of the Hoxnian interglacial forest. It is also significant that Vitis values from one of the fossil pollen cores from Laguna de las Madres contained 30% Vitis in many samples, which would seem indicative of a large population of Vitis, with the likelihood that the plants were being cultivated. Further discussion will be found in Chapter Three.

8) Mobile Dune/Dune Slack Systems

i) Pollen rain of Mobile dune/dune slack system sites D9-12 and Pt0-Pt40 in Doñana National Park

The pollen rain of these communities bears little resemblance to the pollen rain of the vegetation of the fixed dunes. This is mainly caused by the inherent instability of the system with dune fronts moving at a rate of 5-6m yr^{-1} and therefore not allowing the full succession to take place. The pollen rain is dominated by Pinus from the natural populations of Pinus pinea. Pollen types characteristic of this dune system include Liguliflorae, Gramineae, Cyperaceae and Rumex type.

Sites Pt0-Pt40 lie along a transect at 5m intervals, commencing from a Pinus pinea dominated ridge of one contraduna and extending out across a Holoschoenus vulgaris/Carex arenaria dominated slack and onto the Pinus pinea dominated ridge of the next contraduna. The vegetation of the intervening slack is at a pasture type stage with little invasion by any of the main shrub types. The Pinus values on leaving the canopy of Pinus pinea fall very quickly, a common feature found in many samples taken on transects running from woodland to open pasture, (Turner 1964b). In many studies of Pinus pollen rain it has been found that the tree is seriously over-represented (Andersen 1970), and has been found to be very well dispersed (Prentice 1980, Singh et al 1973). Poor representation of Pinus pinea in this study is also to be found in site D11 where nine trees only managed to give a representation of 19% and D110 where one large mature

tree of Pinus pinea only produced 1.8% representation. This seemingly low pollen productivity is surprising for the reasons just mentioned as in the rapid decline in Pinus as one leaves the canopy. A rapid fall in Pinus values is however, not seen in a transect that runs from a plantation of Pinus pinea onto grassland at Laguna de las Madres. The possible cause of the apparently poor representation in the natural systems could result from the trees being relatively immature when sampled or reflecting an ecotypic difference between the natural populations of Pinus pinea and the planted populations.

The transect, on reaching open ground after leaving the canopy of Pinus pinea, goes through local dominance of Liguliflorae, Hypochaeris sp. being the plant responsible for the peak in Pt10 and Leontodon sp. in Pt5. The Liguliflorae peak then gives way to Rumex type dominated sites Pt30 from the local population of Rumex acetosella growing at that point. The high Pinus values of Pt25 is puzzling for Pinus is not recorded from the quadrat, but it was observed that a group of trees of Pinus pinea were growing to one side of the sample quadrat. Throughout the transect the Cyperaceae values are high, reflecting the dominance of Carex arenaria and Holoschoenus vulgaris in the slack of the contraduna. Once again Genista anglica is found to be under-represented, but one of the local Leguminoseae seems to have consistent representation throughout the transect, this is seen in the levels of Ononis baetica type, the likely source being O. viscosa.

Plants of this species were not recorded and it is possible that they were overlooked.

Sites D9-12 were from a more mature contraduna system. Once again the pollen rain is still different from that of the fixed dunes, with low Halimium type and Erica lusitanica type pollen. Despite 33 plants of Genista anglica present in D10 it is still seriously under-represented. The same applies to Ulex minor in D12.

The Artemisia values of D9 are quite characteristic, for Artemisia campestris is a plant that will invade the slacks of the contradunas, rooting in the moist bottom and therefore may be used as an indicator of microclimate.

A common feature of the pollen rain is the amount of non-local pollen input into these Pinus dominated slacks, e.g. Quercus, Eucalyptus, Juniperus, Phillyrea. The Quercus and Phillyrea values are very high, once again pointing to efficient dispersal of these two species, especially Phillyrea, and the likelihood of low local pollen production of the local plants. The amount of non-local input resembles that into the monte blanco/monte negro sites: the vegetation structure is similar in all three cases, so the filtration of pollen by the vegetation is unlikely to be a major factor.

ii) Semi-stablized dune site

One sample was taken from a semi-stabilized dune site.

The vegetation was dominated by Corema album, which is indicative of unstable sunstrate conditions, while the more sheltered parts of the system Genista anglica and Rosmarinus officinalis develop. It can be readily seen that the pollen rain is dominated by Corema pollen and it is also interesting to note the high proportion of Genista type pollen recovered considering that most Genista containing sites observed so far have shown serious under-representation.

iii) Stabilized Dune Slack - Juniperus phoenicia

The sites at Matalascanas represent a more stable sand dune system, one that is stable enough to allow Juniperus phoenicia to invade and it approaches the monte blanco systems. However, the pollen rain does not resemble a monte blanco shrub system for the communities at Matalascanas represent the grazing derived vegetation of the shrub system. High amounts of Anthemis type pollen are recovered from all three sites indicating the large populations of Anthemis sp. present at the site. Site Mal contains high Corema pollen, once again showing the good representation of Corema album. The pollen spectrum of these sites also contains a large amount of Ononis baetica type pollen, a feature already noticed in site Pt0-Pt40, thus not following the normal under-representation of members of the Leguminosae. The plant that gives rise to this pollen type was, however, not recorded from the site, and must have been missed in the vegetational survey of the quadrats. The pollen rain of Juniperus is very low and the reasons for this have already been dealt

with in the section on monte blanco forest vegetation.

Under-representation of many taxa is apparent in these sites, e.g. Armeria pungens, Spartium junceum Urginea maritima, and very surprisingly considering the evidence from N.E. Iran, Artemisia campestris in site Mal. Rosmarinus and Lavandula are represented when present in the quadrat but are still under-represented as in the monte blanco/negro shrub systems. The Halimium values are also low, but reflects the low density of Halimium in the quadrats (see pg. 100)

9) Laguna de las Madres Transect

This set of samples is from a transect which was sampled every 20m (LM1-LM5) from underneath a plantation of Pinus pinea with grassland onto the wet grassland surrounding the plantation at the north of Laguna de las Madres (p.202)

The Pinus data has already been discussed in connection with the dune/dune slack data p.119. It is noticeable that the pollen rain is dominated by Rumex type and Plantago type, these two grassland genera have been found before to be over-represented in the pollen rain (Caseldine 1981). The characteristic under-representation already seen in many genera is repeated here:- Chamaerops humilis, Genista anglica, Pistacia lentiscus and Urginea maritima.

10) Eucalyptus plantation

The one sample taken from such a plantation reveals a very serious over-representation of Eucalyptus in the pollen rain. Pollen has also been observed in the monte blanco/negro shrub

systems and in many of the open structured forest systems, to be a major non-local pollen input and thus Eucalyptus exhibits very good dispersal qualities.

Separation of Mediterranean Plant Communities on the Basis of their Pollen Rain

One of the main aims of surface pollen studies is to permit the recognition of a plant or a community type on the basis of its associated pollen rain. This, if it is possible facilitates the interpretation of fossil pollen assemblages. In the Spanish sites described here it is possible to delimit different vegetation types on the basis of their associated pollen rain, which contrasts with the position described from Iran. Reference to Table 9 shows the main pollen types to be found associated with different communities. For some of the communities it is not possible to characterise them on the basis of their pollen assemblage due to lack of sample material, most of the grazing derived grassland communities come into this category. However, for the shrub and forest systems this has been possible, with one or two exceptions. Indicator species can be used, which show a certain fidelity to particular community types, e.g. Corema album to semi-stabilized sands, Juniperus to monte blanco forest systems and Pinus to unstable dune slacks (though one must be aware of the effect of planted populations of Pinus pinea).

i) Delimitation of grassland systems.

Due to the lack of samples from the majority of the grazing derived grasslands of the shrub systems, this category is the least satisfactory. The one sample taken from the monte negro hygrophytic grassland proved to be too near a portion of the derived shrub

TABLE 9

Identification of Communities on the Basis of their Pollen Assemblage

	Grassland	Shrub	Forest
Monte blanco	*Loeflingia* high+ Cruciferae high+	Halimium high *Mentha* type high *Erica lusitanica* low Non-local pollen high	*Juniperus* high *Pistacia* high
Monte negro	N/A	*Halimium* type high *Mentha* type high *Erica lusitanica* low Non-local pollen high	*Olea* high *Quercus* high *Ceratonia*+
Monte negro hygrophytic	*Illecebrum* high+	*Halimium* type low *Mentha* type low *Erica lusitanica* high Non local pollen high	*Quercus* high *Arbutus* present
Temporary Lagoonal Systems	*Alisma* type high++ *Ranunculus trichophyllos* type+	*Typha latifolia* type high	*Fraxinus* high *Tamarix* high
Mobile Sand Dunes/ Slack	Cyperaceae high *Artemisia* high *Rumex* type high Liguliflorae high	i)m.blanco see above ii)m.negro see above iii)m.n.hyg. see above iv)Unstable:- *Corema*	*Pinus* high N/A N/A

+ indicates a theoretical prediction of delimitation

system and suffered from over-representation of Erica lusitanica type pollen. However, a theoretical delimitation may be made of the grassland types (see Table 3) on the basis of the knowledge of pollen productivity of the species of the different types. Thus the monte blanco grassland would be characterised by high Loeflingia type pollen values, and evidence that high values of this type can occur is to be found in the fossil pollen core from Encinillas Altas. Possibly the Cruciferae input from Malcomia lacera and Brassica barrellieri would also be useful in full delimitation of this grassland type. The monte negro and monte negro hygrophytic grasslands would be difficult to differentiate, the main distinguishing pollen types are poor pollen producers, e.g. Armeria gaditana and Anagallis crassifolia. The different members of the Cyperaceae that characterise each system will also be indistinguishable.The only possibility to distinguish the two communities would be to use Illecebrum type but it is not known what its pollen productivity is. The temporary lagoonal systems which are an extension of the high water levels seen in the monte negro hygrophytic grasslands can easily be characterised by strong concentrations of Alisma type which derive from Echinodorus ranunculoides and also from Ranunculus trichophyllus type from members of the Batrachian section of Ranunculus.

The only other grassland type for which surface samples exist are those from the early stages of dune slack development in the mobile sand dune systems. These

early stages are characterised by high Cyperaceae, Artemisia, Liguliflorae and Rumex type. All derived from plants that commonly invade the early stages of succession (Table 4).

ii) Shrub Systems

The shrub systems have been extensively surveyed and it is possible to delimit them on the basis of their pollen assemblages with one major exception. The easiest to delimit are the monte negro hygrophytic shrub systems (Table 3 and Table 9), these are characterised by very high values of Erica lusitanica type, low Halimium type, low Mentha type and the low input of non-local pollen. The wetter variant dominated by Typha latifolia and Juncus sp. for which no samples have been analysed, but the fossil cores from El Asperillo and Laguna de las Madres indicate high concentrations of Typha latifolia can be obtained,thus indicating that this system can also be distinguished. A major problem exists with the delimitation of the monte blanco/monte negro shrub systems because the pollen rain in both of these communities is similar despite the communities being dominated by different plants. The characteristic pollen rain is low Erica lusitanica type, high Halimium type, Mentha type - 5%, high input of non-local pollen. The reasons for the inability to delimit the two community types are:-

a) Stauracanthus genistioides the characteristic plant of the monte negro produces a pollen type that is indistinguishable from that produced by Genista anglica, a common plant of the monte blanco.

b) In addition to the main distinguishing plants producing the same pollen type, they are seriously under-represented in the pollen rain.

c) The pollen of Calluna vulgaris, a characteristic plant of the monte negro is very well dispersed producing values in the monte blanco that are equivalent to those found in the monte negro.

d) The non-local input into both community types is of the same magnitude.

For the shrub systems of the dune slack vegetation, these will approach the pollen assemblage of the communities from the fixed dune systems as succession progresses. Thus these too may be indistinguishable from the fixed dune shrub systems. Semi-stabilized dune systems can be distinguishable on the basis of the presence of Corema pollen.

iii) Forest Systems

Of the three main types of vegetation the forest systems appear to be more readily distinguishable. The monte blanco forests can be characterised by high Juniperus values, though it must be remembered that sparse Juniperus vegetation will show up very poorly in the pollen rain. On the more silty soils the pollen rain will be characterised by Pistacia values of varying magnitude, depending on the sex of the majority of the plants being sampled. In general it could be possible to delimit such forest communities but the variable

pollen representation of Juniperus (dependent on density) and that of Pistacia (due to dioecy) may prevent this, and thus the pollen spectrum could approach the derived shrub type or grassland type.

The monte negro forests can be clearly delimited, these represent a thermophilous type of forest that is characterised by high Olea pollen and high Quercus pollen. Although no samples were taken from a forest that contained Ceratonia siliqua, a tree that was thought to have been very common in this type of forest in the past. It may be an additional pollen type that could characterise the monte negro forest. However, the tree is a member of the Leguminosae and would almost certainly suffer from under-representation.

The monte negro hygrophytic forests can be distinguished on the basis of high Quercus values, and Arbutus values, despite Arbutus being shown to be under-represented in this community it does exhibit a fidelity to the system and it's pollen is not exported from the community.

The wetter forest variant dominated by Fraxinus angustifolia and Tamarix africana may be differentiated on the basis of these two types but it has been shown that the pollen representation of both types is very variable. However, the presence of high amounts of either should be enough for delimitation of the community since they are both poorly dispersed.

> The forests of the dune slacks are easily characterised on the basis of the large amount of Pinus found in the surface samples, although plantations of Pinus often give the same values, delimitation may still be able to occur on the basis of the ground flora associated with the two types, e.g. invariably shrub vegetation in the natural forests and grassland in the plantations.

Thus compared to Iran, there is great potential for recognizing many of the potential vegetational types that occur in the Doñana area. This is due to the trees and shrubs that constitute the greatest biomass of each site not being as heavily under-represented (compare the sites in Iran dominated by Zygophyllum, Peganum). Over-representation of Artemisia was very common in the Iranian sites but there appears to be little evidence to support this theory for the populations of Artemisia campestris in Doñana.Other similarities revolve around the Leguminosae which show under-representation in both regions and in the potential of certain plants that could be used on the basis of their fidelity to certain plant communities, e.g. Pyrus bourgeana and Smilax aspera, but could not be used due to serious under-representation (compare pollen types like Thalictrum and Ceratocephalus type in Iran).

Pollen Transport in the Communities of the Doñana Area

Pollen transport in the vegetation types of the Doñana area present a different picture from that of N.E. Iran. Tauber (1965 and 1967) models of pollen transport in woodland are more applicable here, not only in relation to certain woodland and shrub communities due to differences in vegetational structure.

a) Pollen movement in shrub communities

Pollen transport and movement in the shrub communities depends on:-

i) Structure of the vegetation
ii) Pollen productivity
iii) Position of flowers
iv) Time of flowering

With highly open, structured shrub communities like the monte negro and monte blanco, these sites will tend to receive increased non-local pollen input, since only a small amount of pollen filtration will occur on imported pollen. The amount of non-local pollen may be accentuated if the pollen productivity of these sites is low. Pollen movement within the system will also be relatively unhindered, as a consequence of the open vegetation structure. Contrast this state of affairs with the monte negro hygrophytic shrub systems, here the vegetation presents a dense closed structure that is capable of heavy filtration of imported pollen and thus the non-local pollen input would be reduced. The possibility of higher pollen productivity in such communities would also reduce the

amount of non-local pollen input. The movement of pollen within the system will also be affected by the closed structure. This would manifest itself in plants that discharged their pollen into the trunk space component, i.e. plants that flower at low levels, either ground dwelling plants or those that flower on older stems although the plant may be conspicuous component of the canopy, having their pollen movement hindered and thus the chance of any of these pollen types being exported from the system will be lessened. On the other hand if the plant flowers in the canopy, its pollen will be discharged into the canopy component of pollen flow and thus move freely and be exported from the system with ease. Pollen movement within the system will be reduced for any plant that does flower in the canopy because any pollen discharged on entering the vegetation would face the same problems that any non-local pollen type would find, i.e. filtration and pollen productivity of the trunk space flowering plants. This may be the reason why Phillyrea is found in greater quantities in areas such as the monte blanco/negro where the shrub is absent.

b) Forest communities

Pollen movement within these communities will also depend on the four factors affecting pollen movement in the shrub systems. Thus the open structured sites such as the monte blanco and monte negro would allow free pollen movement at trunk and canopy component levels. The open structure combined with the low pollen productivity of the Juniperus and Pistacia dominated

forests will also allow a higher input of non-local pollen. The effect of the density of trees has also been shown to have an effect on pollen movement with sparse densities of trees producing little representation and thus a deficit of pollen that can be exported (Cf. Juniperus). Position of the flowers will be of little importance due to the open structure and consequential free movement of pollen. The monte negro hygrophytic forests present a different picture, for this forest type is dominated by Quercus suber and is a closed structure. The import of pollen would be affected by the filtering effect of the closed canopy. There might be a trunk space component of pollen flow comparable to temperate deciduous woodland, but the presence of heavy liana components such as Smilax aspera and Rubia peregrina would reduce pollen movement in the trunk space as just seen in the derived shrub community. This may be the reason for Arbutus showing a particular fidelity to this community type, for Arbutus as an understorey would discharge its pollen into the trunk space. The effect on Phillyrea another common understorey tree would be the same and populations of Phillyrea growing in the trunk space components of forest communities may not be as well represented as those growing in the canopy components of shrub communities. If the liana populations were removed then trunk space movement of pollen would again be of importance.

Compared to the N.E. Iran studies, the amount of long distance pollen transport (i.e. over 100km) into the Donana sites is very much reduced and restricted to a few grains of the following genera:- Alnus, Corylus, Betula, Ephedra. The higher pollen productivity of these semi-arid sites from S.W. Spain than those from N.E. Iran could be the reason for this state of affairs. The pollen movement in Iranian sites was thought to depend largely on ground water movement of pollen, this component in the present studies is of little consequence.

The time of flowering does not assume as great an importance as in temperate deciduous woodlands, where early spring flowerers would be better represented in the pollen rain than summer flowerers due to the canopy closing and reducing the amount of export of pollen, For the communities examined here are of an evergreen nature and thus conditions for movement would be the same the year round unless different wind patterns at different stages of the year assume importance.

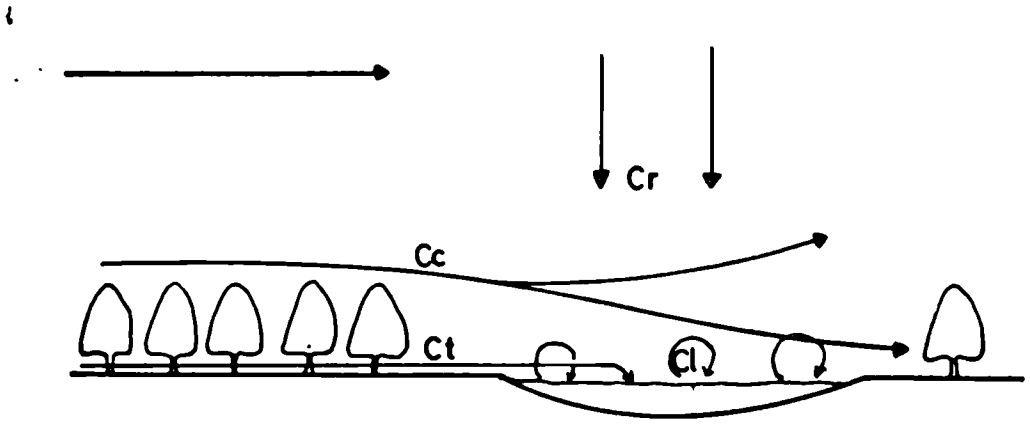
Pollen movement into sites of deposition

If the above points about the variation in pollen movement in the various communities are true then the pollen input into a depositional site like Laguna de las Madres will also be affected, depending on the vegetational community surrounding the Laguna at any one time (Fig.23-24). The proportion of the various components that make up the pollen rain, i.e. trunk space, canopy component etc. will also vary in relation to the position of the site in relation to the surrounding vegetation and also on the size of the site (Fig.23-24). It is possible that the main pollen input into a small laguna from a Quercus/Smilax community may be a canopy component rather than the normal trunk space component expected in the case of a small lagoon, for trunk space movement in the Quercus forest may be reduced due to heavy liana populations. In larger lagoons the canopy component would anyway be a dominant feature of the pollen input (Fig.23-24). The canopy component of monte negro hygrophytic shrub systems would also follow the same pattern for in these communities the trunk space is reduced due to the structure of the vegetation. Thus plants discharging into the trunk space will be poorly represented. If a monte blanco/negro forest or shrub system were present around the site then the pollen representation in small lagoons may be a trunk space component while with the larger lagoons a canopy component would dominate. The amount of long distance pollen transport will depend on the local pollen productivity of the local vegetation on the site.

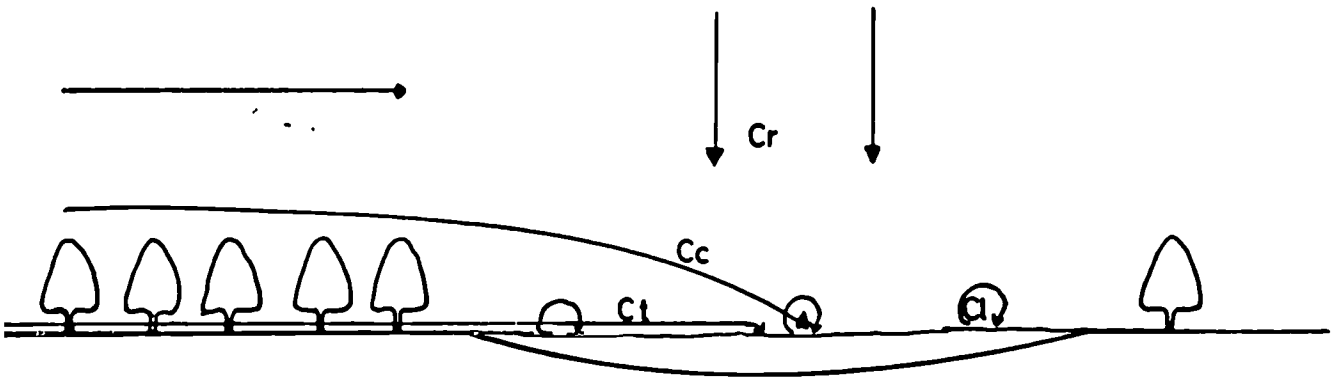
Fig.23

Pollen Flow in

Monte blanco/Monte negro - Shrub/Forest Vegetation



Small Basin

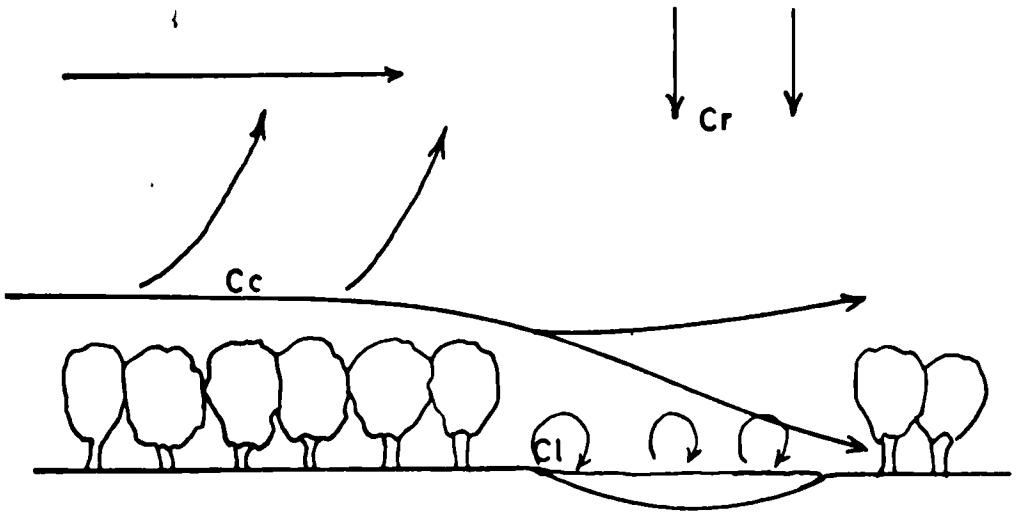


Large Basin

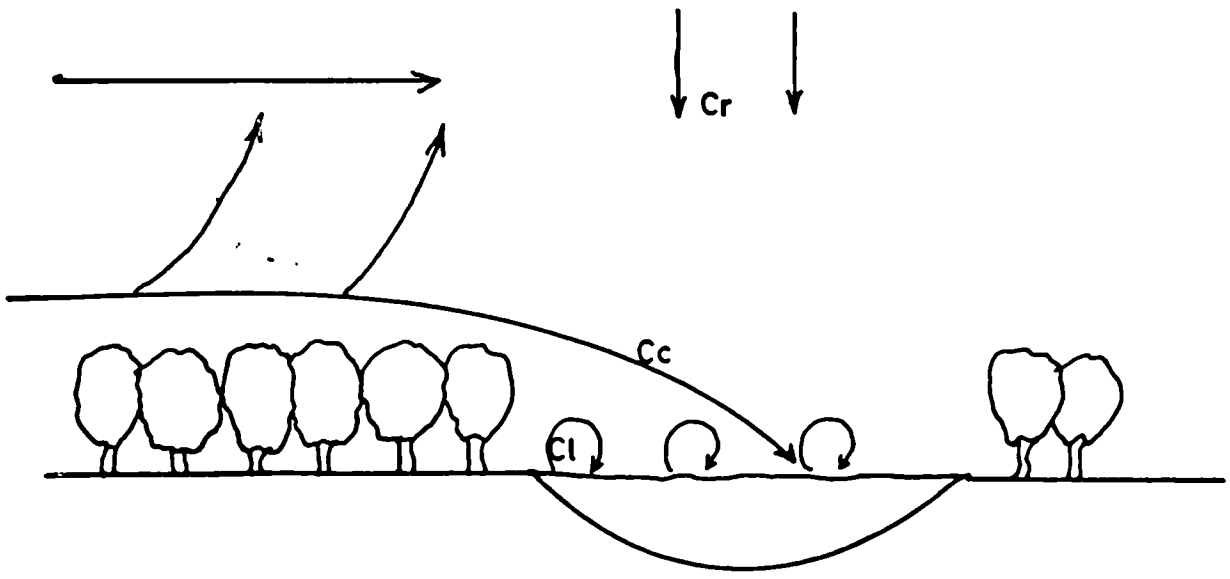
Fig.24

Pollen Movement in

Monte negro hygrophytic - Shrub/ Forest Vegetation



Small Basin



Large Basin

CHAPTER THREE

Fossil Pollen Cores from El Asperillo

Exposed along the coast between Torre del Oro (018077) and Matalascanas (167984) is a series of ancient sand dune systems known as "Arena Gordas". The systems have been found to contain a series of stratified bands of a peaty/sandy nature. The stratigraphy of the bands is found to vary along the coast, sometimes there is only a single band apparent and at other points three or more bands are evident. Overlying these ancient dunes occur more recent dunes which have now been stabilized by vegetation particularly Corema album. This more recent dune system was extensively forested by Juniperus phoenicia, but this vegetation cover has been removed and the area replanted with Pinus pinea (G. Novo, personal communication). The whole cliff section is experiencing active erosion of the cliff face by the wind and sea, the area of sand accretion having moved 20km further down the coast to the Donana National Park.

The age of these ancient sand dunes is a source of some controversy. The detailed geomorphology of the coastline is described in a paper by Vanney and Menanteau (1979) who favour a Wurmian age of the sands. The I.G.M.E. (1975), however, regard the peat sequence as somewhat older but do not suggest a specific period and refer to their deposition as being Plio-Quaternary times, a very considerable period of time. Preliminary pollen analyses of three samples from the peat bands by Caratini and Viguier (1973) lead them to

propose an Atlantic age for the deposits, on the basis of the presence of 0.5% Corylus pollen and the absence of any plants indicative of cold climates. They also found large quantities of Pinus pollen as well as Salix, Ericaceae, Compositae and a few grains of Ephedra and Betula. They thus correlate the deposition of the peat bands with the beginning of deposition in Laguna de las Madres. They did not take into account the possibility of long distance transport causing the Corylus input, a point which is discussed in greater detail in the concluding section to this chapter. The I.G.M.E. however, say that, on account of the geomorphology of the system, the stratified bands must predate the formation of peat in Laguna de las Madres and therefore cannot represent a deposit of Atlantic age. Recent radio-carbon dating of material from the system has given a date of 30,000 B.P. for the base of the sequence and a date of 13,000 B.P. for one of the bands (Menanteau, personal communication) One must however, be aware of the limitations of radio-carbon dating so near to the sea with the likelihood of contamination by other older carbon sources and thus leading to older dates in error, as well as the inherent limitations of the method. If the dates are representative then they put the formation of the system into the late Quaternary and the formation of the peat bands earlier than that proposed by Caratini and Viguier (1973). Thus the base is thought to have formed in the middle of the last glaciation of Europe and the peat bands to have been laid down at the end of the last glaciation. A detailed stratigraphy is given of a section at El Asperillo I.G.M.E. (1975[a]). Above the peat bands are three red ferruginous bands of sands and at certain points along the coast, erosion has left evidence of iron fossilized roots above the

peat bands. Deposits of other minerals are also found above the peat bands in places, most notably deposits of Manganese. There has been some uplifting of the dunes (Menanteau, personal communication) and the sea was on average 2km further out than at present during the last glaciation.

Since the sequences were proved to contain sufficient countable pollen and since they predate the formation of peat in Laguna de las Madres (I.G.M.E. 1975), it was decided to make a thorough investigation of the peat bands in order to:-

a) Ascertain the vegetational processes occurring in the sequence

b) Gain knowledge about the distribution of the main forest types in S.W. Spain at the time of deposition.

Part (a) was fully answered but for reasons that will become apparent, the answers to part (b) remain somewhat ambigious, although tentative suggestions are made.

Methods

Four sites were chosen at which to investigate the peat bands:- As2, As3, As4, As5. As2 and As3 represent a single band, As4 two bands and As5 three separate bands. The positions of the sites and the position of each band in the stratigraphy of each site is given in Figs.30-44 . The bands were sampled in situ, using a clean knife blade each time to remove approximately $1cm^3$ of material every 2cm down the chosen band. The samples were transferred to a labelled clean sealable polythene bag for transportation by air back to London, where they were stored at $2^{\circ}C$ in the dark until required for analysis. Contamination of the samples at the site by modern pollen rain, was checked by collecting the sandy material which was windblown along the cliff face. These samples when prepared gave no evidence of contamination by any modern day pollen. The samples were prepared according to Appendix B except that:-

i) The HF phase was extended to 36 hours boiling plus 3-4 days soaking.

ii) $6cm^3$ of 10% HCl was added and allowed to boil for 3 minutes before centrifugation and decantation of the supernatant, before the HF treatment to prevent excessive carbonate reaction when HF was added to the tubes.

Part of the sample was subjected to loss on ignition to provide information about the organic matter content of the sample. Weighed samples that had been dried overnight in an oven at $100^{\circ}C$ were placed in a muffle furnace at $600^{\circ}C$ and

left for approximately three hours. The samples were transferred to a desiccator to allow to cool down before final weighing, from which the percentage organic matter was calculated.

At least 500 land pollen excluding Cyperaceae were counted from each level and identifications of pollen made according to keys in Moore and Webb (1978), for types not represented in these keys see Appendix A where keys and descriptions are given to some of these types. The resultant pollen diagrams are given in Figs.25-44.

All the pollen values are expressed as a percentage of the Total pollen less the Aquatics and Cyperaceae. The Aquatics are expressed as a percentage of the Total pollen less the Cyperaceae and the Cyperaceae as a percentage of the Total pollen. The loss on ignition of most of the samples is given on the diagrams. The pollen diagrams have been zoned conventionally, the delimiting types for the zones are found in Tables 10-13.

TABLE 10

ASPERILLO 3

BASIS FOR ZONATION

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
As3-6	Gramineae-*Pinus*-	*Pinus* falls, Gramineae increase Chenopods peak. Organic matter low.
As3-5	*Pinus*-*Artemisia*	*Pinus* rises, *Artemisia* peaks, Cyperaceae increase. Organic matter low.
As3-4	*Halimium*-*Erica*-*Pinus*	*Pinus* falls, *Halimium* peaks, *Erica*, *Corema* both peak, *Serratula* present. Organic matter falls.
As3-3	*Pinus*-Cyperaceae	*Pinus* rises, Gramineae fall steeply, *Ranunculus acris* type present, Liguliflorae fall, Cyperaceae increase. Organic matter increases.
As3-2	*Pinus*-*Artemisia*-	*Pinus* falls slightly, Gramineae rise, Liguliflorae high, *Asphodelus* present Organic matter low.
As3-1	*Pinus*-*Corema*-Cyperaceae	*Pinus* increases, Gramineae fall, Cyperaceae, *Corema* high. Organic matter low.

Fig.30

Asperillo 3 - Stratigraphy

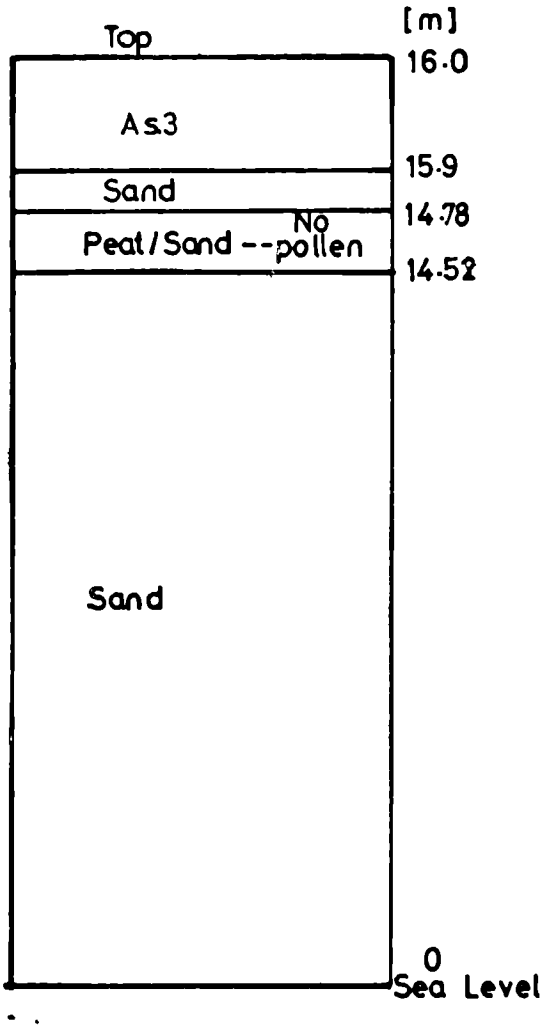


Fig.25

Asperillo 3

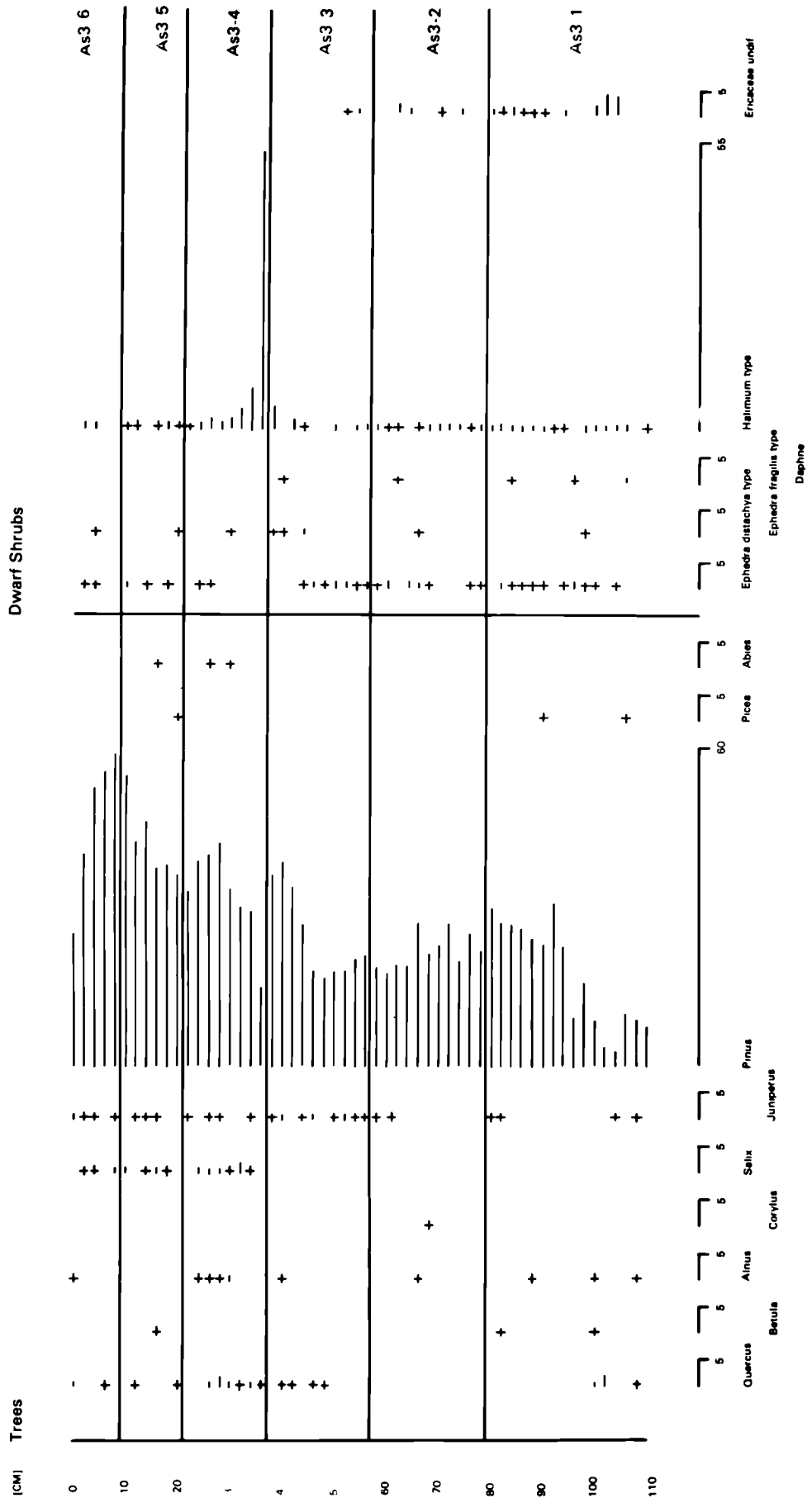


Fig.26

Asperillo 3

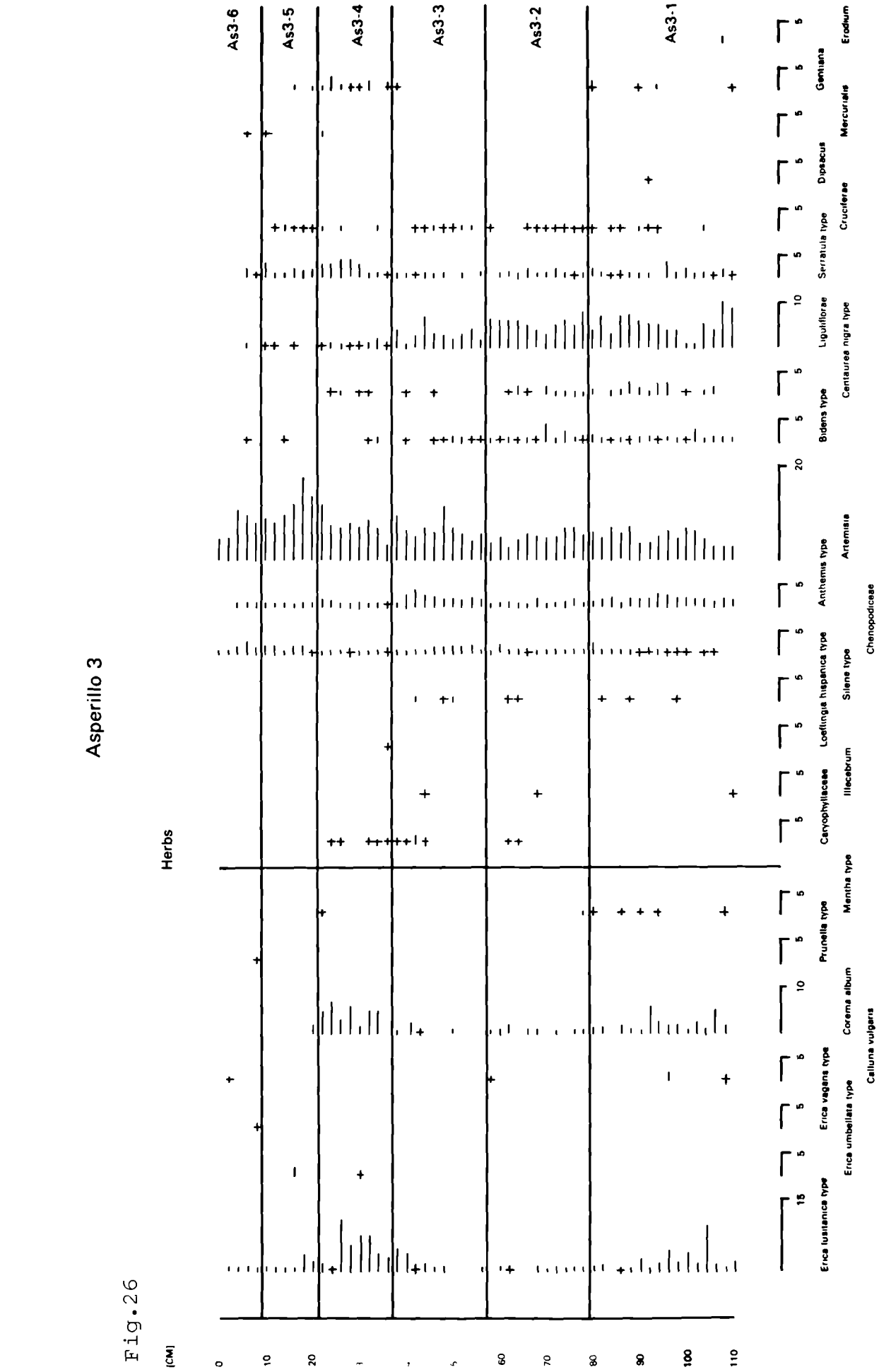


Fig.27

Asperillo 3

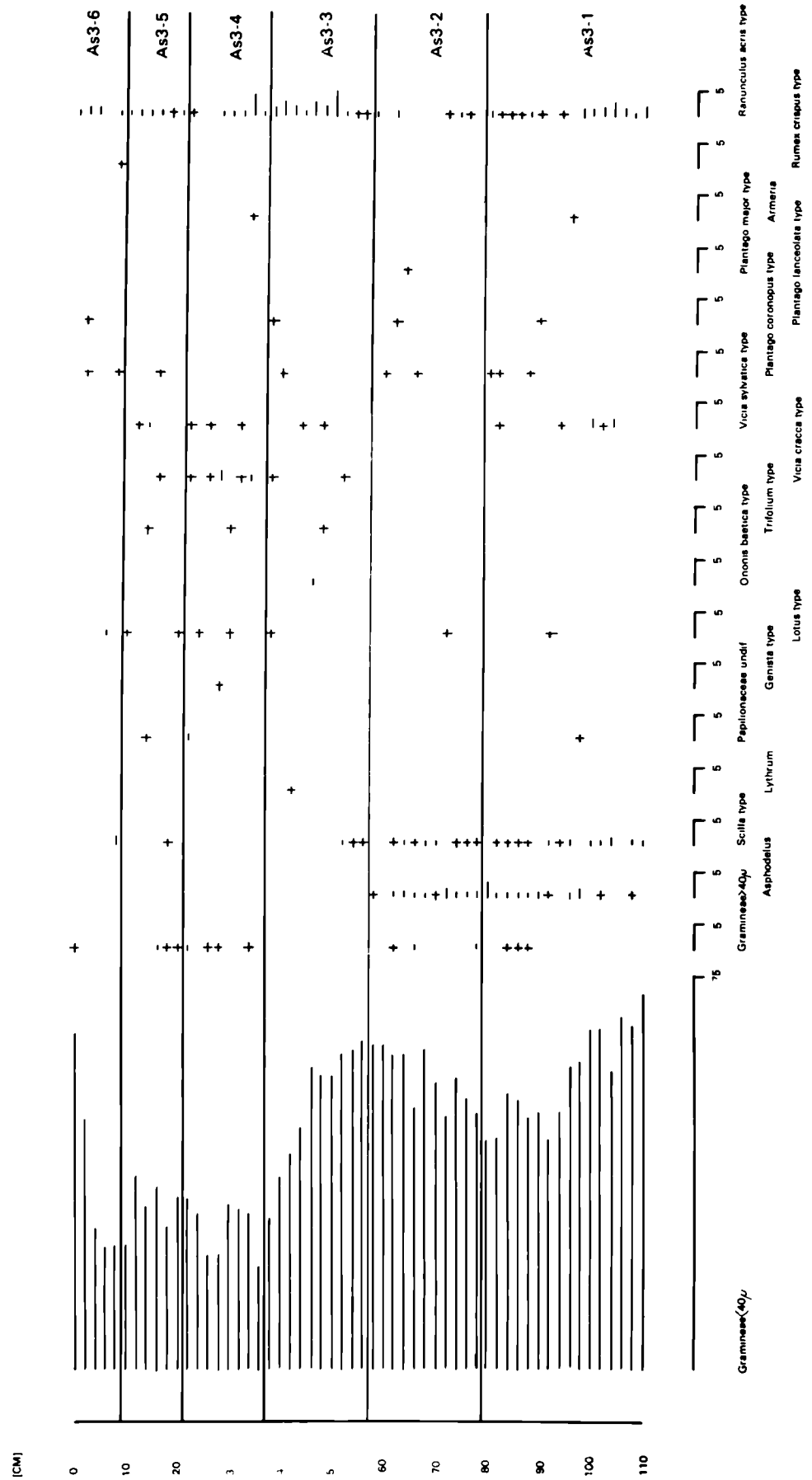


Fig.28

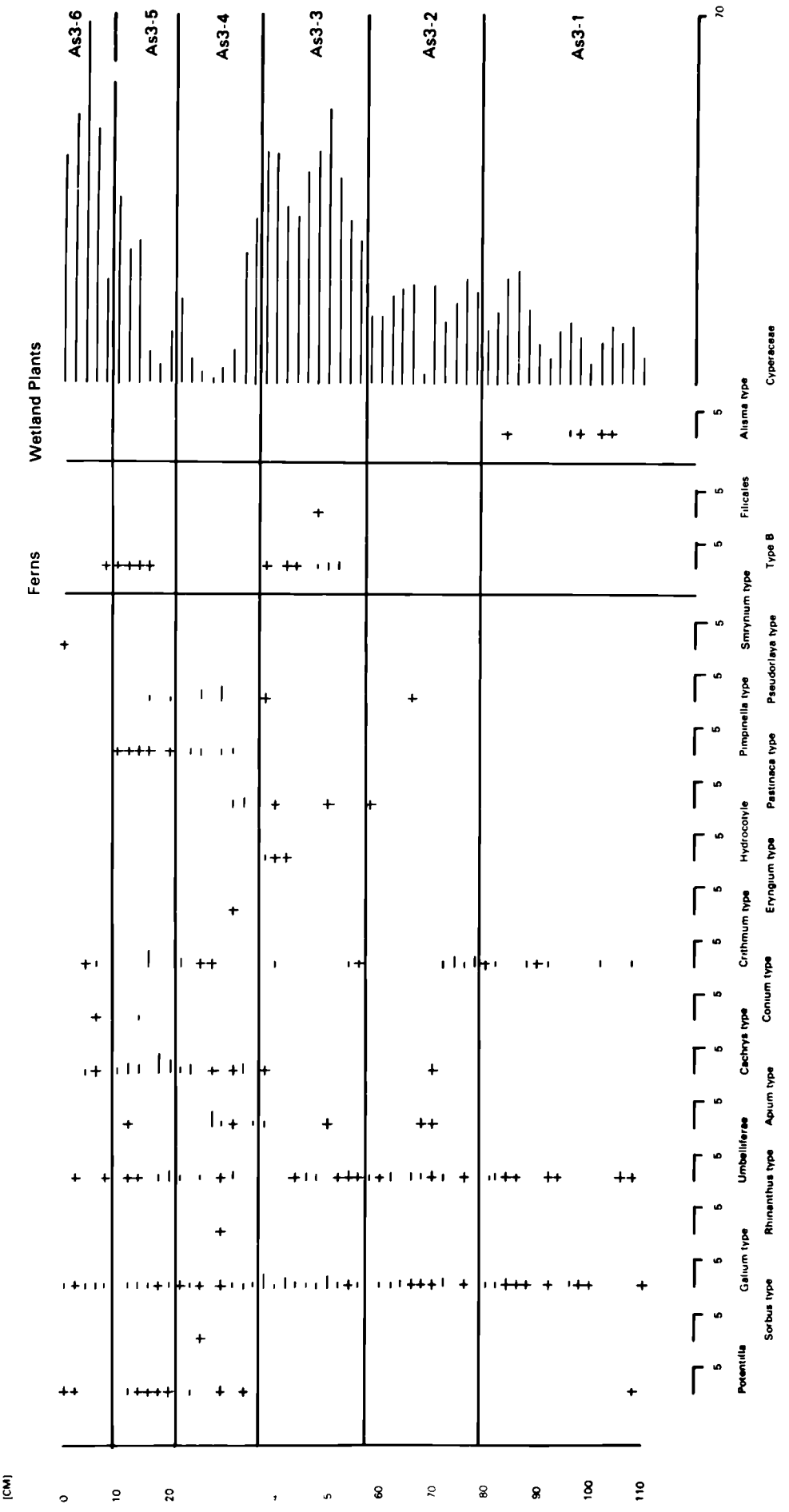
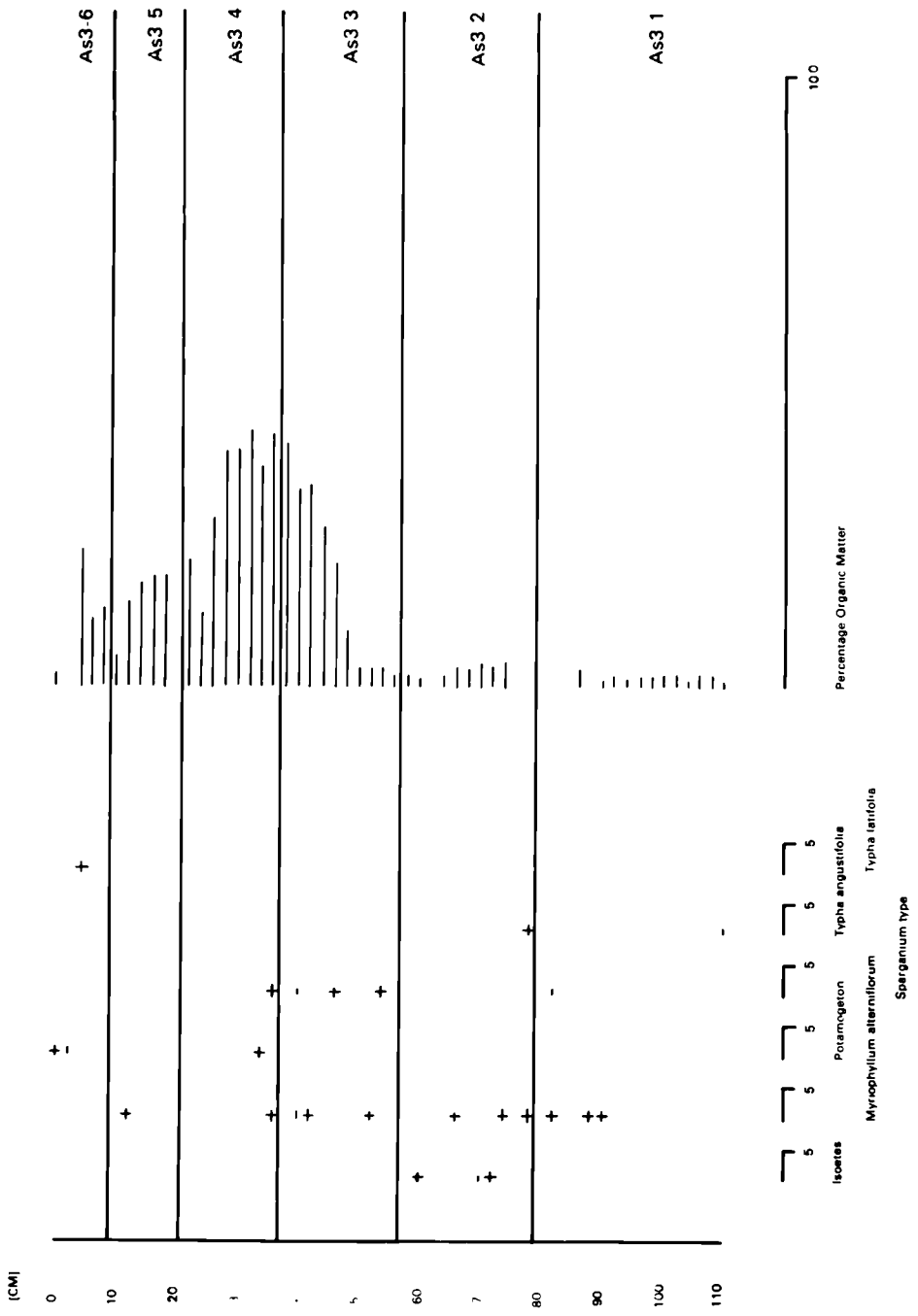

Asperillo 3
(CM)
Ferns
Wetland Plants
As3-6
As3-5
As3-4
As3-3
As3-2
As3-1
Potentilla
Sorbus type
Gallium type
Rhinanthus type
Umbelliferae
Apium type
Cachrys type
Conium type
Crithmum type
Eryngium type
Hydrocotyle
Pastinaca type
Pimpinella type
Pseudorlaya type
Smyrnium type
Type B
Filicales
Alisma type
Cyperaceae

Fig.29


Asperillo 3
As3-6
As3 5
As3 4
As3 3
As3 2
As3 1
(CM)
0
10
20
60
80
90
100
110
100
Percentage Organic Matter
5
5
5
5
5
5
Isoetes
Potamogeton
Typha angustifolia
Typha latifolia
Myriophyllum alterniflorum
Sparganium type

Asperillo 3

The results of the pollen analysis from this core are given in Figs.25-29. The zonation schema is to be found in Table 10. The stratigraphy of the band is given in Fig.30.

Pollen assemblage zone As3-1

Throughout this zone the rise in Pinus occurs associated with a concomitant fall in the pollen values of Gramineae. The relatively low Pinus pollen figures suggest, in comparison with the modern day pollen rain of Pinus that the nearest Pinus trees is probably at least 15m away at the beginning of the zone and closer still at the end of the zone. The rise in Pinus values may also reflect a growing proportion of the young seedlings, reaching sexual maturity. The vegetation at this point in the site is still of an open structure, the Pinus canopy not having closed, since there are high percentages of herbs present, e.g. Liguliflorae, Artemisia.

There are few indications of any shrub development, pollen of Erica lusitanica type variable in this zone, the peaks may indicate the existence of a monte negro hygrophytic shrub community nearby. Corema pollen values are also variable and the peaks may indicate that certain areas of the site had not fully stabilized.

There appears to be indications of flooding occurring in this zone as indicated by:- pollen of Alisma type, Sparganium type, Typha angustifolia, Myriophyllum alterniflorum, Cyperaceae. Echinodorus ranunculoides is the plant that is probably giving

the Alisma type input. It is a common plant of the wet slacks and lagoons of the Doñana area today. Cyperaceae pollen probably derives from Holoschoenus vulgaris, a common plant in wetter areas (Table 4). The pollen values found would indicate that it could be a dominant plant at this point in the site (from comparison with modern day populations of Holoschoenus vulgaris). Carex arenaria, a plant of the drier more mobile sands and of the first contra-dunas, could also be contributing to the Cyperaceae pollen input. The high values of Artemisia also corroborate the above, since it too is a plant that roots in the more humid parts of the slacks today (Table 4) Allier et al (1974). The presence of E. lusitanica type would also indicate the existence of high water tables.

Pollen of Armeria and Scrophularia are found to be low and absent respectively, these plants are commonly found as first invaders of new stretches of dune slack left by the retreating dune fronts. However, it has been shown that both of these types are under-represented in the pollen rain and thus are unlikely to show up.

Pollen of Asphodelus was also found to be a constant feature of this zone and once again could indicate the existence of damper areas in this part of the site. As has been seen from the modern pollen survey it has been found to be seriously under-represented in the pollen rain and may have been an important component of the vegetation at this time. The existence of humid areas in slacks are known to prevent the invasion of Pinus and may have been keeping the populations low (Figueroa 1976).

It seems that the site at this time represents an early phase in the successional sequence to full Pinus forest. Conditions indicate the existence of more humid areas in which more hygrophytic plants are living, the slack of a contraduna could provide such a habitat. The Pinus population is probably colonising the drier tops of the contradunas. The organic matter content of the soil at this stage in the development of the site is very low, a common feature of early successional stages after the cessation of dune movement.

Pollen Assemblage Zone As3-2

This zone exhibits a slight reversion on the part of Pinus, with the Gramineae rising at the same time. Conditions in the site still appear to be open and appears to be damper than the previous zone, the presence of Isoetes indicates the existence of extensive winter flooding. This increased flooding could have reduced the population of Pinus trees (Figueroa 1976), where Pinus is unable to colonise the wet hollows due to lack of water tolerance, and will only colonise slacks and contradunas of a drier nature. The organic matter content of the soils are still low during this zone, showing that no great change in soil development has occurred since the previous zone. Despite the evidence for increased wetness the shrub systems especially the Erica dominated ones have not responded.

Pollen Assemblage Zone As3-3

This zone is characterised by a heavy increase in Pinus values as well as a steep decrease in values of the Gramineae. A heavy increase is also seen in the Cyperaceae curves. The

rise in Pinus represents a continuing increase in the population of trees at this point in the site. From comparison with modern day pollen samples from Pinus communities, the populations are quite large and may indicate the existence of a closed canopy of Pinus. The increase in Pinus could be the reason for the drop in Gramineae and Liguliflorae as both these become intolerant to competition from Pinus. Populations of Holoschoenus may also be expanding in this zone, indicating the almost complete dominance of this plant in a more hygrophytic portion of the site and pollen of Asphodelus disappears from this zone.

There appears to be still no development of shrub vegetation as yet in this zone. Values of Erica and Halimium type remain low until the end of the zone when they begin to increase. The amount of organic matter in the soil now also increases steeply, indicating soil development possibly indicating conditions similar to those of the monte negro/ monte negro hygrophytic shrub systems of the fixed sand dunes.

Pollen Assemblage Zone As3-4.

The fall in Pinus found at the beginning of this zone associated with peaks in many other taxa such as Erica lusitanica type, Corema album, Serratula type, and especially Halimium type, represents a severe perturbation of the Pinus forest. This perturbation appears to have been initiated at the end of the last zone as Halimium and Erica lusitanica type start to increase here. The Pinus forest however, recovers from the effects of this perturbation, the likely cause of which is probably fire, which today in the Doñana National Park often results in the same kind of sequences seen. Halimium

halimifolium is a pyrophytic species ready to invade by seed, the rich, temporarily fertilised ground formed by the fire. It is found to form extensive populations after about five years (G. Novo 1977), before the vegetation reverts to something approaching its original state. Other plants also seem to be helped by the fire and the system at this point reverts to a situation very similar to that of monte negro shrub vegetation. The Corema peak may also be accounted for by the effects of fire, for fire would temporarily remove vegetation cover and thus destabilize the soil surfaces in the drier parts of the site, which then provides ideal situation for Corema to invade. Members of the Liguliflorae and Gramineae do not appear to be able to take advantage of the open conditions created by the fire and in fact Liguliflorae pollen values now almost totally disappear. The vegetation for the remainder of the zone still resembles that of monte negro shrub vegetation, but soon the Halimium type values are reduced to their original levels and afterwards the values of Erica lusitanica type and Corema also return to their previous state, though the process is not completed until the next zone.

It is interesting to note that one grain of Genista type was recovered from the middle of this zone. As has been demonstrated in the modern pollen survey, pollen of this type in particular is under-represented in the pollen rain and one must entertain the possibility of large stands of e.g. Genista anglica or Stauracanthus genistioides in this phase of the vegetation of the site.

Pollen Assemblage Zone As3-5

In this zone Pinus values approach their highest level and represent the formation of a closed canopy of Pinus, thus decreasing the herbaceous plants, e.g. Gramineae growing underneath the canopy. The increase in Pinus values could represent an increasing input of new trees into this part of the site, this is thought unlikely since values of Artemisia rise further, which indicates extensive wet areas in the site.

The temporary monte negro shrub type vegetation formed in the previous zone has now disappeared and the community reverted to a "Pastizal" type of vegetation (i.e. grassland type). The reasons for this reversion are unknown, but a possible cause could be grazing, for, as seen on the fixed dune system of Doñana National Park today the shrub systems give way under heavy grazing to grassland (G. Novo 1979). However, the reason could also be a nutrient deficiency problem, the fire providing enough nutrients to enable shrub colonisation to occur, but as the nutrient reserve is used up and leached, the soil can no longer support shrub vegetation and reverts back to pasture type vegetation.

Pollen Assemblage Zone As3-6

This zone is characterised by a steep decline in Pinus values associated with increased Gramineae representation. The sequence is then terminated at the top of the zone by non polleniferous sands. The implication of these two occurrences by comparison to the present, where flooding is associated with the onset of a dune front (G. Novo 1979) suggests that here we are seeing the swamping of this part of the site with mature

Pinus forest, by a front of invading dunes (Plate 2 and 3). Thus, in general the vegetational sequence follows that for the modern day slack sites with some important differences:-

i) Lack of any permanent shrub development towards the end of the succession apart from a temporary phase associated probably with an increased nutrient supply due to a fire

ii) Long distance pollen input:- Values of *Quercus* and *Phillyrea* are low compared to modern day sites, but there were higher inputs of *Betula*, *Alnus*, *Corylus* *Salix*, *Juniperus*, *Picea*, *Abies*. The continued presence of an input of *Ephedra distachya* type is also noteworthy, considering the almost total lack of *Ephedra* input into modern day sites. These features of the long distance pollen input will be developed later in the chapter.

The life of the site must have been too short to allow any invasion by *Juniperus* since nowadays this is the normal course of events on the dry soils (Harrant and Jarry 1967), however, it must be remembered that *Juniperus* when present as scattered trees, is under-represented. Thus two possibilities exist: the continuous input of *Juniperus* pollen indicates either a few trees present in the site which are under-represented (Cf. Mal,Dd4) or the existence of a scattered population producing a relatively constant input near the site. This point will be expanded later in the chapter.

Asperillo 3 - discussion

We can observe the following distinctive features of the pollen rain during the deposition of the core from Asperillo 3:-

i) *Pinus* rises throughout the diagram and drops steeply at the top of the core, except for a perturbation in the *Pinus* curve in zone As3-4

ii) Values of *Halimium*, *Juniperus*, *Quercus* are all generally low.

ii) Values of Cyperaceae, Gramineae, *Artemisia* and Liguliflorae are all high.

With the above information it should be possible to try and see if there is an analogue to these vegetation features, to be found in the modern day pollen samples from most of the vegetation types. On looking at Table 9 which gives the main distinguishing features of the pollen rain from each main vegetation type, we can see that the vegetation in the core on the whole does not seem to correspond to any of the shrub types (except for certain sections). The lack of any permanent high values of *Halimium* type *Erica lusitanica* type, *Juniperus* and *Quercus* seem to preclude the monte blanco/negro/negro hygrophytic shrub and forest systems from being an analogue. The closest analogue to the pollen sequence seen in the core, is that of the surface samples from the mobile sand dune/dune slack systems found in the Doñana National Park, i.e. those sites dominated by *Pinus pinea* as a conse-

quence of the dynamics of the mobile sand dune system. Thus the sequences seen in the pollen core from Asperillo appear to represent a sequence from such a system each band being terminated by the arrival of the next sand dune. The rest of the cores from Asperillo also follow parts of the sequence seen in As3 to a greater or lesser extent, with As3 representing the full sequence. Now that a suitable model exists against which to base the vegetation sequences seen in the cores. It is now possible to go through the cores in some detail and look for similarities to add differences from the present pollen rain, to see if the dune/dune slack model is a suitable one to invoke for the vegetation sequence seen in the cores.

Before entering detailed discussion it will be helpful if the major vegetational changes during succession and the process of dune movement are noted. A resumé of the main features of dune movement are given on pg. 64 . Reference also to this section will give full vegetation successional details and the factors affecting the course of succession. A brief resumé will be given here.

Once the dune has passed, recolonisation of the dune tail takes place. The first plant invaders are usually Armeria pungens, Carex arenaria, Artemisia campestris, Malcomia littores and Scrophularia frutescens. Artemisia campestris often colonises the first contraduna associated with Holoschoenus vulgaris both of which root in the humid bottoms of the slack and are sensitive to being buried by fresh sand. Then depending on the depth of the water table, there develops vegetation similar to that of the fixed dunes, i.e. monte

Plate 3

View of the dune front swamping mature Pinus pinea

Plate 2

View of the dune front invading a dune slack

blanco/monte negro etc. Table 4 gives the course of events under different water regimes. The contradunas themselves become colonised by Pinus pinea seedlings normally at the second contraduna stage. Allier et al (1974) have shown that the contradunas contain Pinus of increasing age, the maximum age attained by the pines being a direct function of their distance to the second contraduna; this relationship is so precise that it permits calculation of the average advance of the dune system. At the base of the slacks the new dune front invades the vegetation which has colonised it, which may contain trees greater than 40 years old and 15m high. The Pinus trees are normally completely buried and the majority eventually die. Once the dune passes reconstruction will again begin to start at the base of the tail of the dune (first contraduna). Therefore the Pinus pinea forest, perfectly adapted to the early colonising of permanent surfaces left by the dunes in passing, fail to stabilize the dune systems in Doñana. Plates 2 and 3 illustrate the succession. Fast dune movement thus prevents the invasion of the modern day slacks by Juniperus since its life cycle is too long in comparison with the dune/slack cycle.

Details of the modern day pollen of these slack systems will be found on p .119.

The general vegetational sequences are known for the modern day mobile dune systems and will now be compared with the sequences observed in the Asperillo diagrams.

TABLE 11

ASPERILLO 4

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
As4-7	Myriophyllum alterniflorum-Artemisia-Chenopodiaceae	Pinus falls steeply, Chenopod, Artemisia and most of aquatics all peak.
As4-6	Pinus	Pinus high, Liguliflorae decrease. Organic matter higher.
As4-5	Pinus-Liguliflorae	Pinus peaks, Liguliflorae high, Anthemis high. Organic matter low.
As4-4	Liguliflorae-Anthemis-Gramineae	Liguliflorae high, Bidens high. Anthemis high, Gramineae high. Organic matter low.
As4-3	Cyperaceae-Juniperus-Artemisia	Pinus collapses, Juniperus increases, Artemisia increases, Cyperaceae high. Organic matter variable.
As4-2	Pinus-Liguliflorae Halimium	Pinus peaks, Halimium peaks, Erica falls, Liguliflorae high. Organic matter variable.
As4-1	Pinus-Erica-Cyperaceae	Pinus increases, Erica high and falls, Gramineae decrease, Cyperaceae high.. Organic matter increase.

Fig.32

Asperillo 4 – Stratigraphy

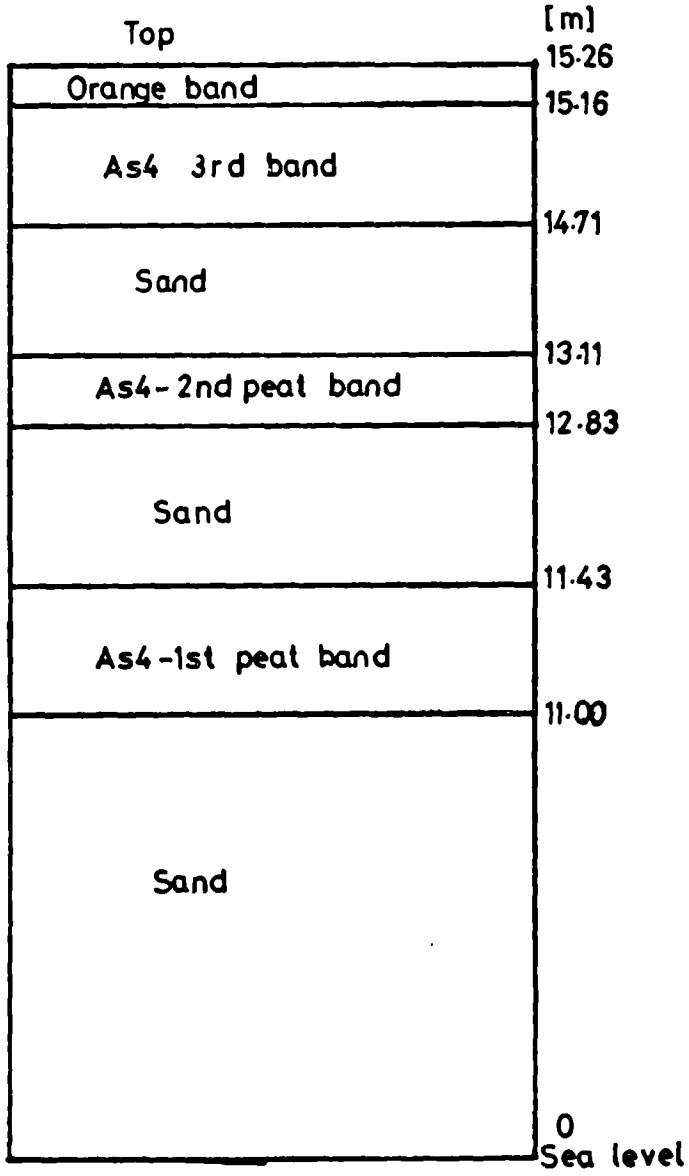


Fig.33

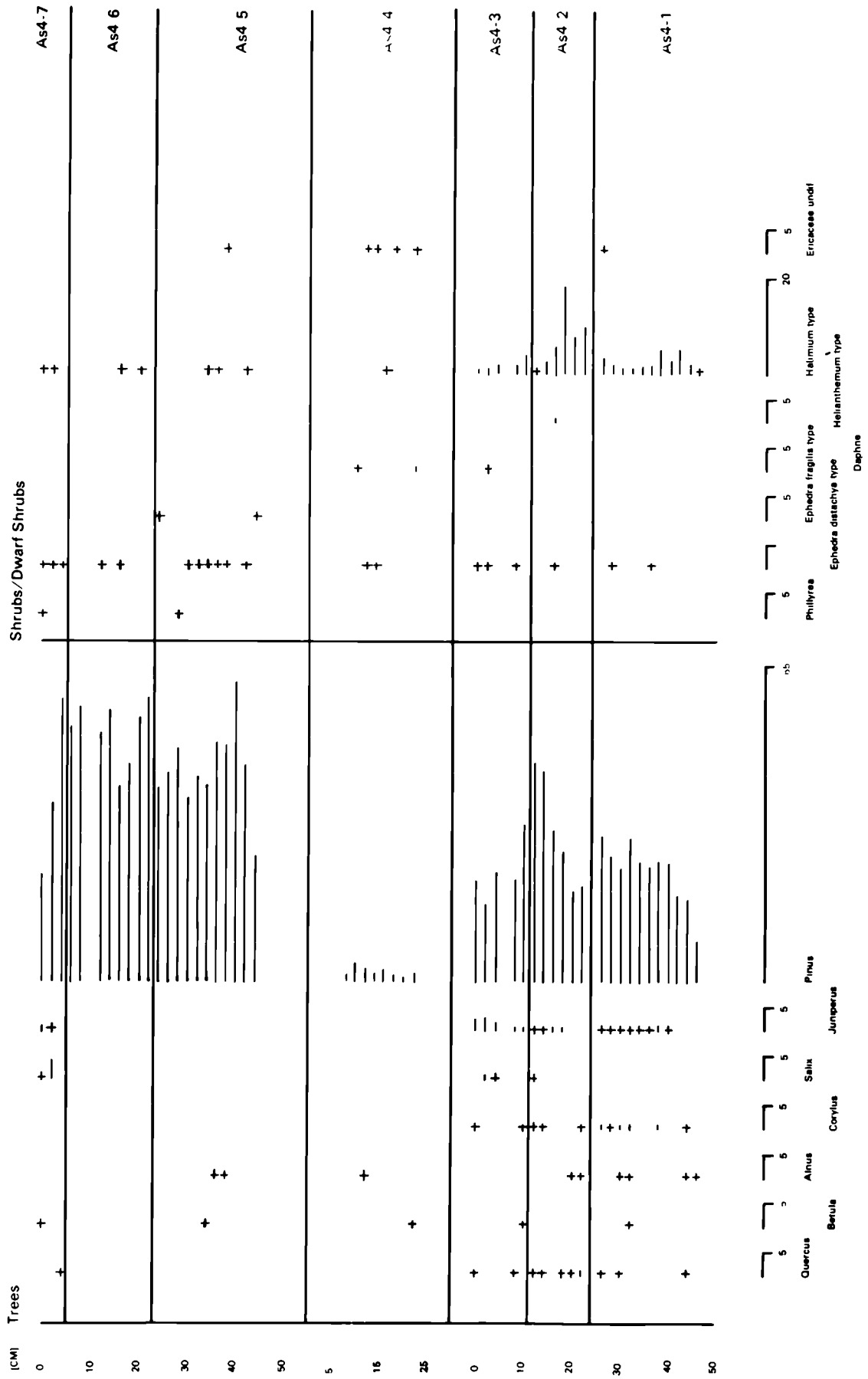

Asperillo 4
Shrubs/Dwarf Shrubs
Trees
(CM)
As4-7
As4 6
As4 5
As4 4
As4-3
As4 2
As4-1
Quercus
Betula
Alnus
Corylus
Salix
Juniperus
Pinus
Phillyrea
Ephedra distachya type
Ephedra fragilis type
Helianthemum type
Helianthemum type
Daphne
Ericaceae undif

Fig.34

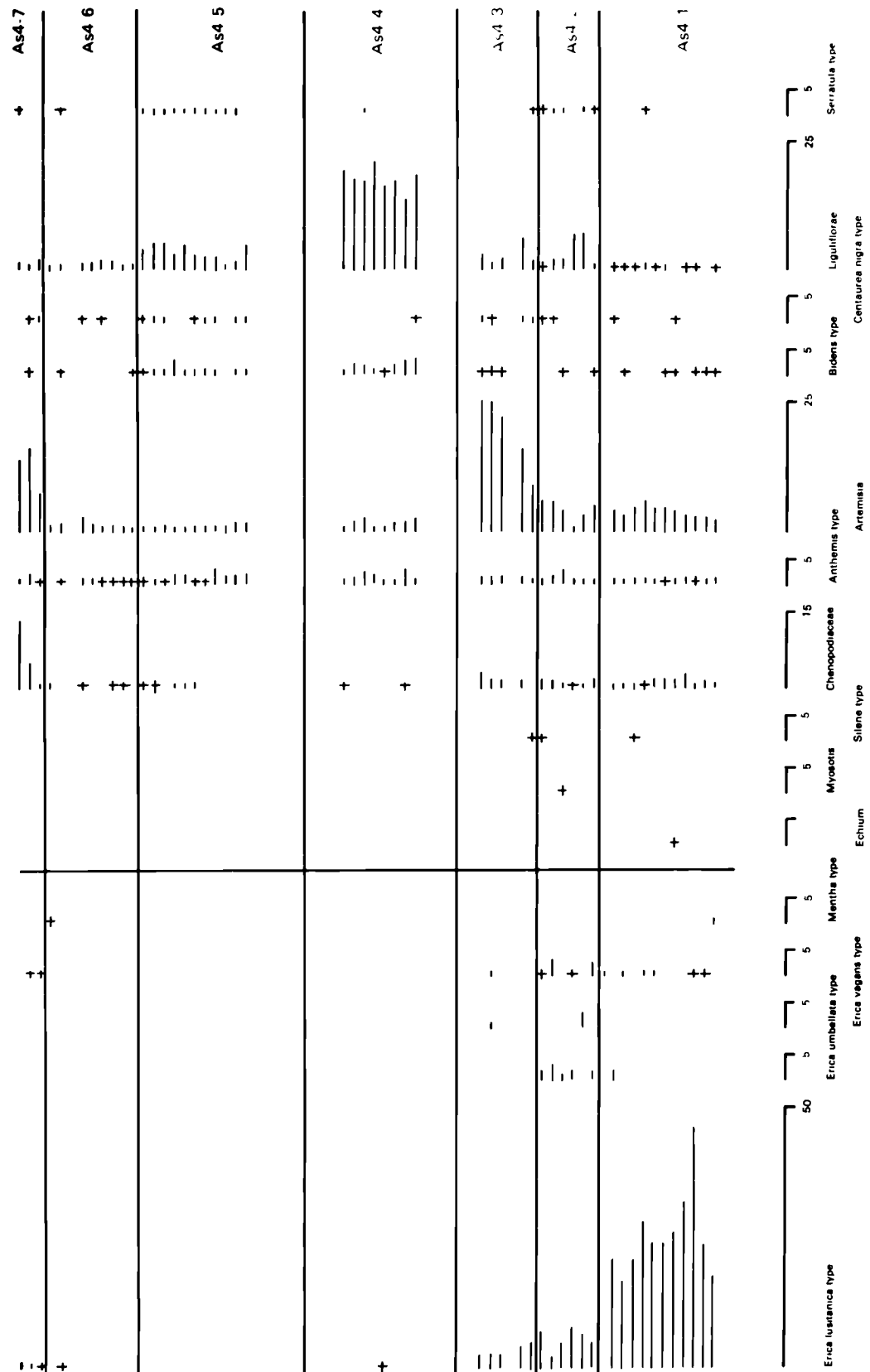

Asperillo 4
Herbs
(CM)
As4-7
As4 6
As4 5
As4 4
As4 3
As4 2
As4 1
Erica lusitanica type
Erica umbellata type
Erica vagans type
Calluna vulgaris
Mentha type
Echium
Myosotis
Silene type
Chenopodiaceae
Anthemis type
Artemisia
Bidens type
Liguliflorae
Centaurea nigra type
Serratula type

Fig.35

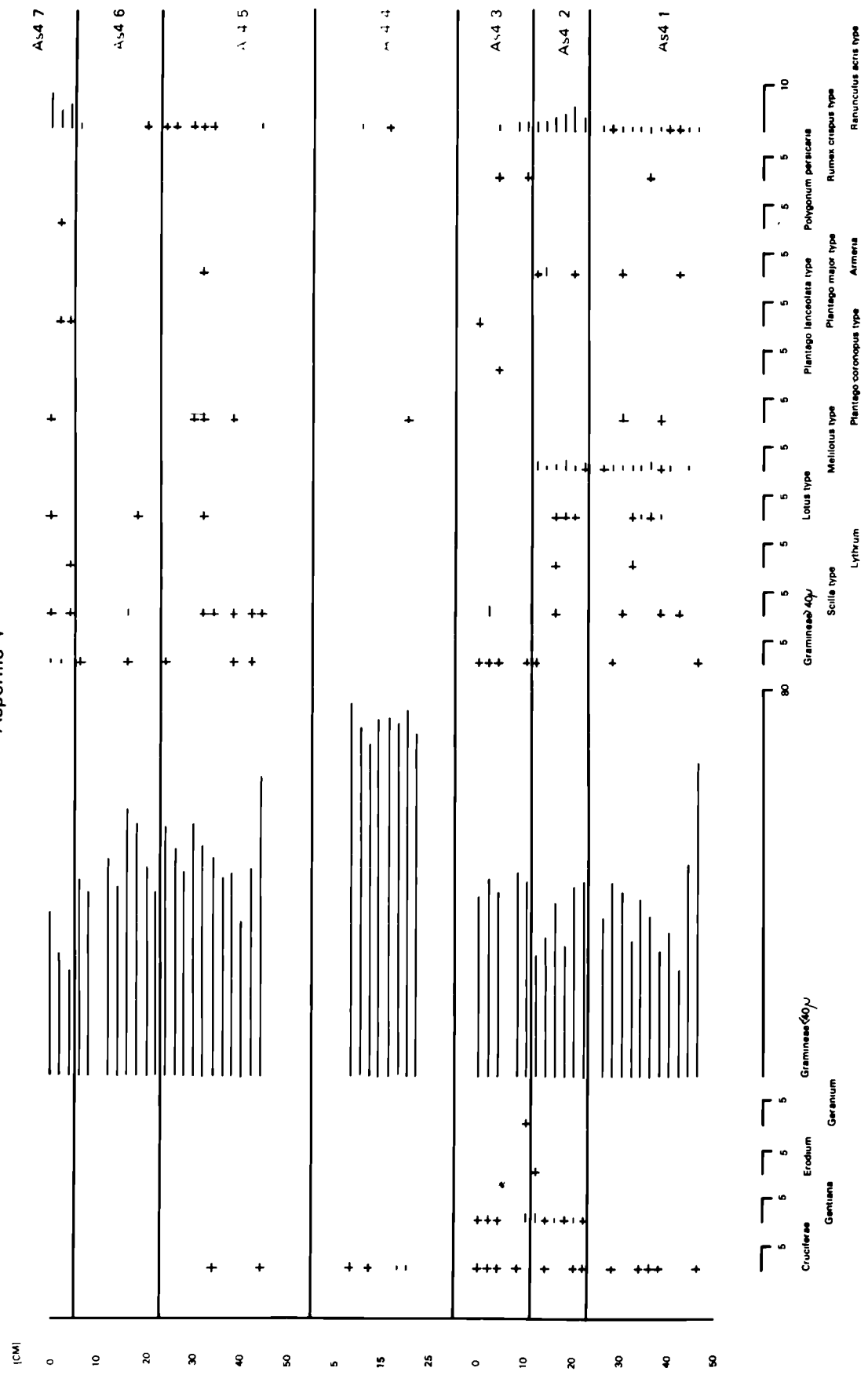
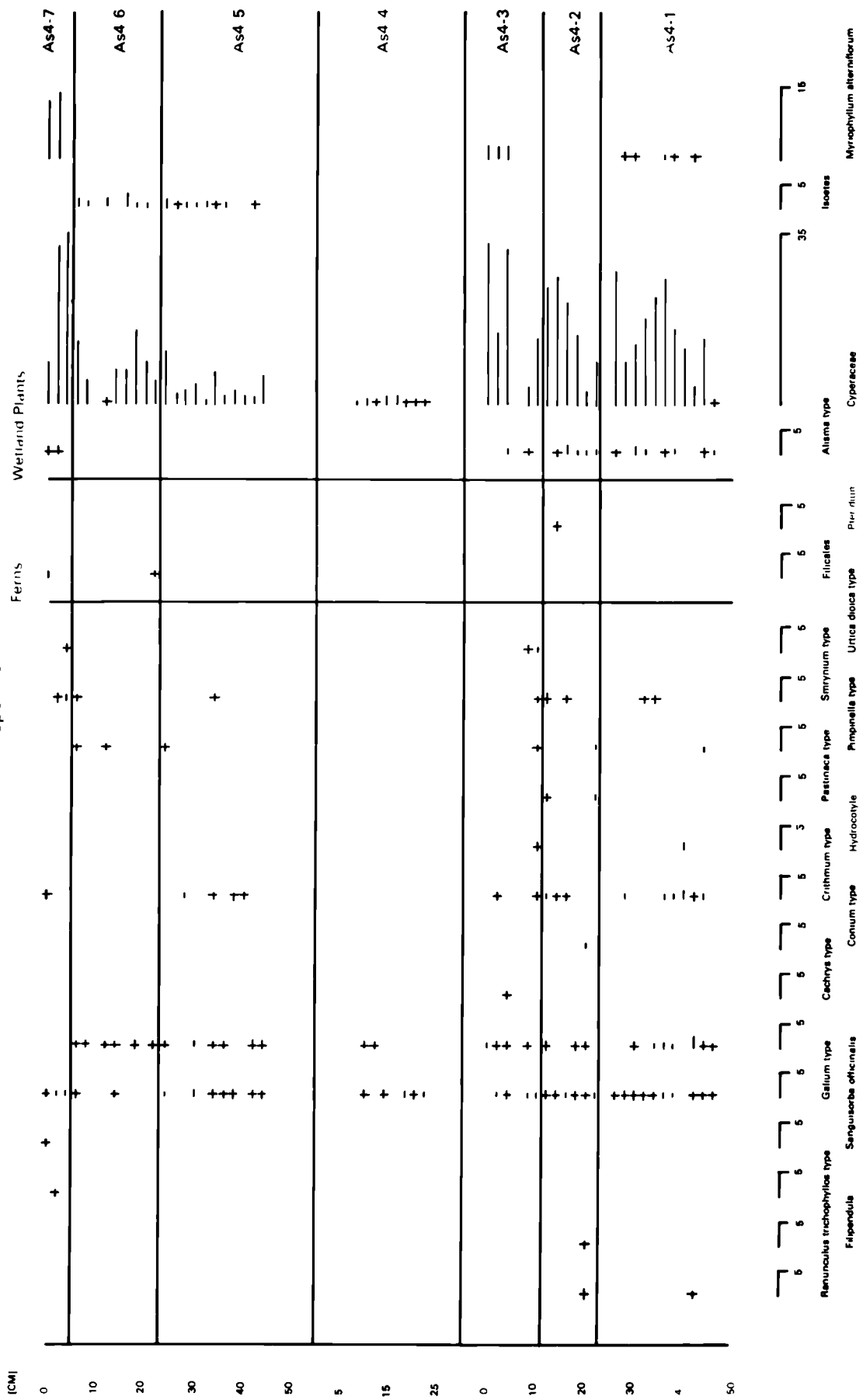

Asperillo 4
As4 7
As4 6
As4 5
As4 4
As4 3
As4 2
As4 1
(CM)
0
10
20
30
40
50
5
15
25
0
10
20
30
40
50
Cruciferae
Gentiana
Erodium
Geranium
Gramineae 40µ
Gramineae 40µ
Scilla type
Lythrum
Lotus type
Medicago type
Plantago coronopus type
Plantago lanceolata type
Plantago major type
Armeria
Polygonum persicaria
Rumex crispus type
Ranunculus acris type

Fig.36


Asperillo 4
Ferns
Wetland Plants
As4-7
As4 6
As4 5
As4 4
As4-3
As4-2
As4-1
[CM]
Ranunculus trichophyllos type
Filipendula
Sanguisorba officinalis
Potentilla
Umbelliferae
Galium type
Cochrya type
Conium type
Crithmum type
Hydrocotyle
Pastinaca type
Pimpinella type
Smyrnium type
Urtica dioca type
Filicales
Alisma type
Cyperaceae
Isoetes
Myriophyllum alterniflorum

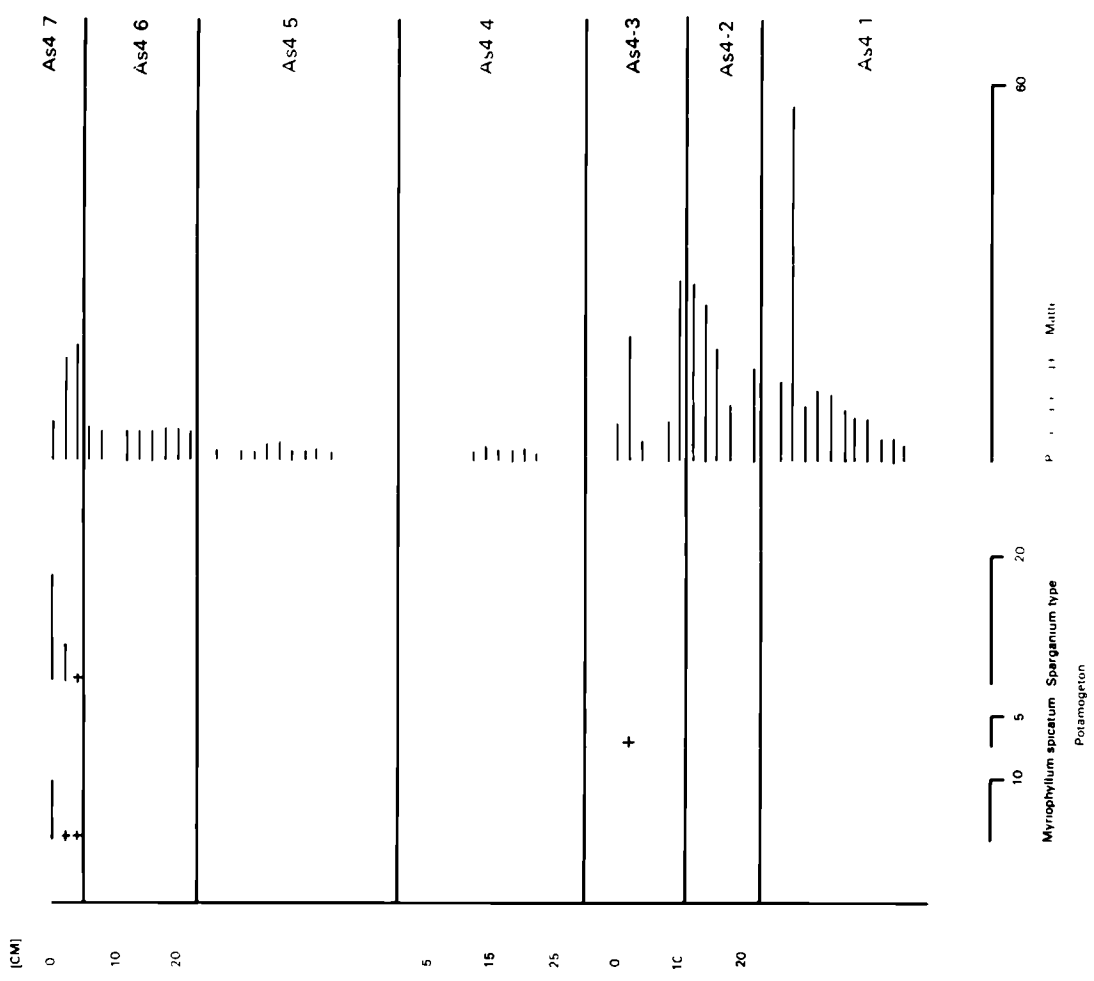

Asperillo 4
As4 7
As4 6
As4 5
As4 4
As4-3
As4-2
As4 1
[CM]
0
10
20
5
15
25
0
10
20
10
5
20
60
Myriophyllum spicatum Sparganium type
Potamogeton

Fig.37

Asperillo 4

This site is situated at GR088035 and was found to contain three definite peat bands (Fig.32). All three bands are presented in the pollen diagrams Figs.33-37. As4-1 - As4-3 representing the first band, As4-4 representing the second band, As4-5 - As4-7 representing the third band. Each band will now be discussed in turn. The basis for zonation will be found in Table 11.

First Peat Band

Pollen Assemblage Zone As4-1

This first zone of the bottom band presents a different picture from that seen in the band system at As3. Here Erica lusitanica type is high and Halimium type present in relatively high amounts. Certain pollen types present in this zone are indicative of humid conditions:-

i) Erica lusitanica type, a type that derives from E. scoparia, a common plant of the monte negro hygrophytic shrub of the fixed sand dunes.

ii) Alisma type, again as in As3 derives from Echinodorus ranunculoides, a plant of wet habitats

iii) Myriophyllum alterniflorum another aquatic species.

iv) Cyperaceae, pollen probably derives from Holoschoenus vulgaris a common plant of the humid slack bottoms.

Thus it seems that this portion of the slack at As4 was wetter

than that seen in As3, this does not, however, imply that the whole slack would have been wetter. Other parts may have experienced different water regimes from those seen in this part of the slack. The zone shows a progressive increase in Pinus representation, associated with a decrease in Erica lusitanica type and the Gramineae. This probably represents the population of Pinus reaching maturity and the beginning of a shading effect.

Pollen Assemblage Zone As4-2

This band shows a steep drop in Pinus values at the beginning of the zone (followed by a strong recovery to even higher levels) and Erica lusitanica type full, from the previous zone, while Halimium type peaks at the beginning. Three possibilities exist for these effects:-

i) The water table has fallen, producing a change in shrub vegetation from monte negro hygrophytic, dominated in the pollen rain by Erica lusitanica type to that of a monte negro/blanco type. But this does not explain the fall in Pinus, which prefers low water tables; also Mentha type pollen does not increase which one would normally find in a monte negro/blanco shrub vegetation.

ii) The second possibility is that a fire has occurred in the slack at this point. This would lead to falls in Pinus and Erica lusitanica type as both are destroyed by fire. Invasion by Halimium, Liguliflorae and Corema (on the destablized sands) would then follow as seen in modern day sites (G. Novo 1977) and in the peat band from As3.

iii) A third possibility could be a combination of lowering water tables allowing Pinus to invade the site occupied by Erica since Pinus prefers the drier soils and cannot tolerate high water tables, associated with Erica dominated vegetation. Then conditions became susceptible to fire as a consequence of the fall in water table and the subsequent fire allowed Halimium and Liguliflorae to invade the slack at this point. If the change in water table has occurred, this may well explain the continued depression of Erica even after the rest of the vegetation had recovered in this zone.

With the perturbation past Pinus climbs to its highest levels, indicating conditions that are very suitable for it. Further evidence that the soils are drier in this zone compared to the previous zone come from the absence of Myriophyllum which had formed a consistent input into the previous zone.

Pollen Assemblage Zone As4-3

This zone is marked by a steep drop in Pinus values, associated with plants indicative of wet conditions, e.g. Myriophyllum alterniflorum, Artemisia and Cyperaceae, which suggests widespread flooding which nowadays, heralds the approach of the next dune front. The decreasing Pinus is a result of intolerance to waterlogging of the roots.

There may be some indication that Pinus is giving way to Juniperus towards the end of the zone for, as seen in As3, values for Juniperus increase slightly and as has already been mentioned, this could indicate the existence of a population of Juniperus occurring in the contemporaneous

slack, which may not have been as transient as modern day slacks. The dune fronts could also be moving more slowly than is found today, thereby increasing the life of the slack and allowing the development of conditions that are sufficently stable over an adequate time for Juniperus to invade.

The long distance pollen component of the pollen rain during the time of this band has a constant input of Corylus and Ephedra distachya type, the presence of Betula and Alnus input and the low Quercus input in comparison to modern day sites.

Second Peat Band:- As4-4

The vegetation of this band is indicative of totally open, dry conditions, since high Gramineae, Liguliflorae and Bidens type values are found, perhaps due to the presence of Ammophila, Hypochaeris and Helichrysum respectively. This open vegetation of Liguliflorae and Bidens type is not recorded from modern day sites and is a point of difference between the fossil and modern day sites. Trees may have not been present in the slacks history. It is also observed that no other changes towards Pinus forest take place and it is thought that this process did not occur in this slack. Another possibility is that the rest of the sequence was removed by erosion before being covered by the dune front that separates this band from the one above.

Third Peat Band As4-5 - As4-7

Pollen Assemblage Zone As4-5

This zone shows a rapid expansion of pine pollen values which is maintained throughout the zone. Erica lusitanica type pollen is absent and Liguliflorae values are high. The values of Pinus indicate (by comparison with modern day pollen studies) a heavy cover of Pinus in the site. The absence of Artemisia and Erica lusitanica type indicate that the site may well have been dry during this zone, perhaps drier than the conditions found in As4-2 when Pinus last achieved its maximum. Isoetes is present throughout the zone, which is indicative of some winter flooding occurring in the slack of the contraduna whilst Pinus is restricted to the ridges (drier). Organic matter content is also low, a feature often found in the dry monte blanco soils of the fixed sand dunes.

Pollen Assemblage Zone As4-6

The Pinus values in this zone go even higher but are variable. The Liguliflorae have once again decreased, as is commonly found in these diagrams after a spell of importance from the lower regions. The soils appear to be undergoing increased development, with an increase in organic matter of the band, which may be associated with increased water tables, for Isoetes becomes more frequent as does Artemisia.

Pollen Assemblage Zone As4-7

Pinus values in this zone undergo a heavy fall associated with increases in aquatic species, e.g. Myriophyllum alteriflorum, M. spicatum, Sparganium type, Cyperaceae. In comparison to the present day dune systems this degree of development of

swamp vegetation is not found. The site at this stage must have had a permanent or semi-permanent lagoon dominated by these plants. It is also possible that trees of Salix may have been present, although the cause of the input could be the result of long distance transport from a perturbated watershed from outside the system. The termination of the diagram was caused by swamping by the next dune front.

Once again the band is characterised by a constant input of Ephedra distachya type pollen but does not have the constant input of Corylus seen in the first band. Inputs of Quercus and Alnus are also lower than those found in the first band.

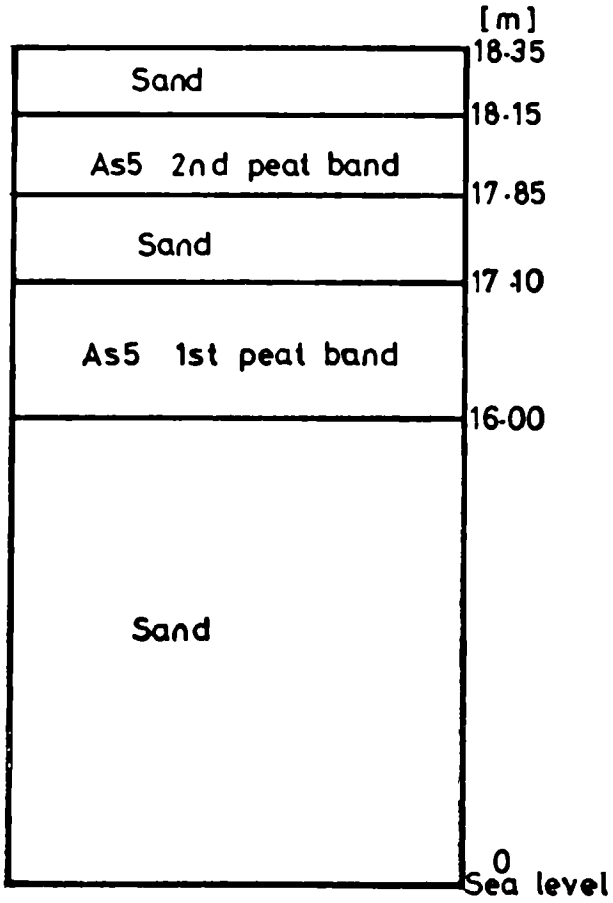
TABLE 12

ASPERILLO 5

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
As5-4	Artemisia-Anthemis-Potamogeton	Artemisia high, Anthemis high Liguliflorae fall, Potamogeton high.
As5-3	Pinus-Liguliflorae	Pinus peaks, Liguliflorae rises, Gramineae fall.
As5-2	Pinus-Gramineae	Pinus peaks, Liguliflorae falls, Gramineae very high.
HIATUS	HIATUS	HIATUS
As5-1	Pinus-Artemisia-Cyperaceae	Pinus variable, Artemisia peaks Cyperaceae peak.

Fig.38

Asperillo 5 - Stratigraphy



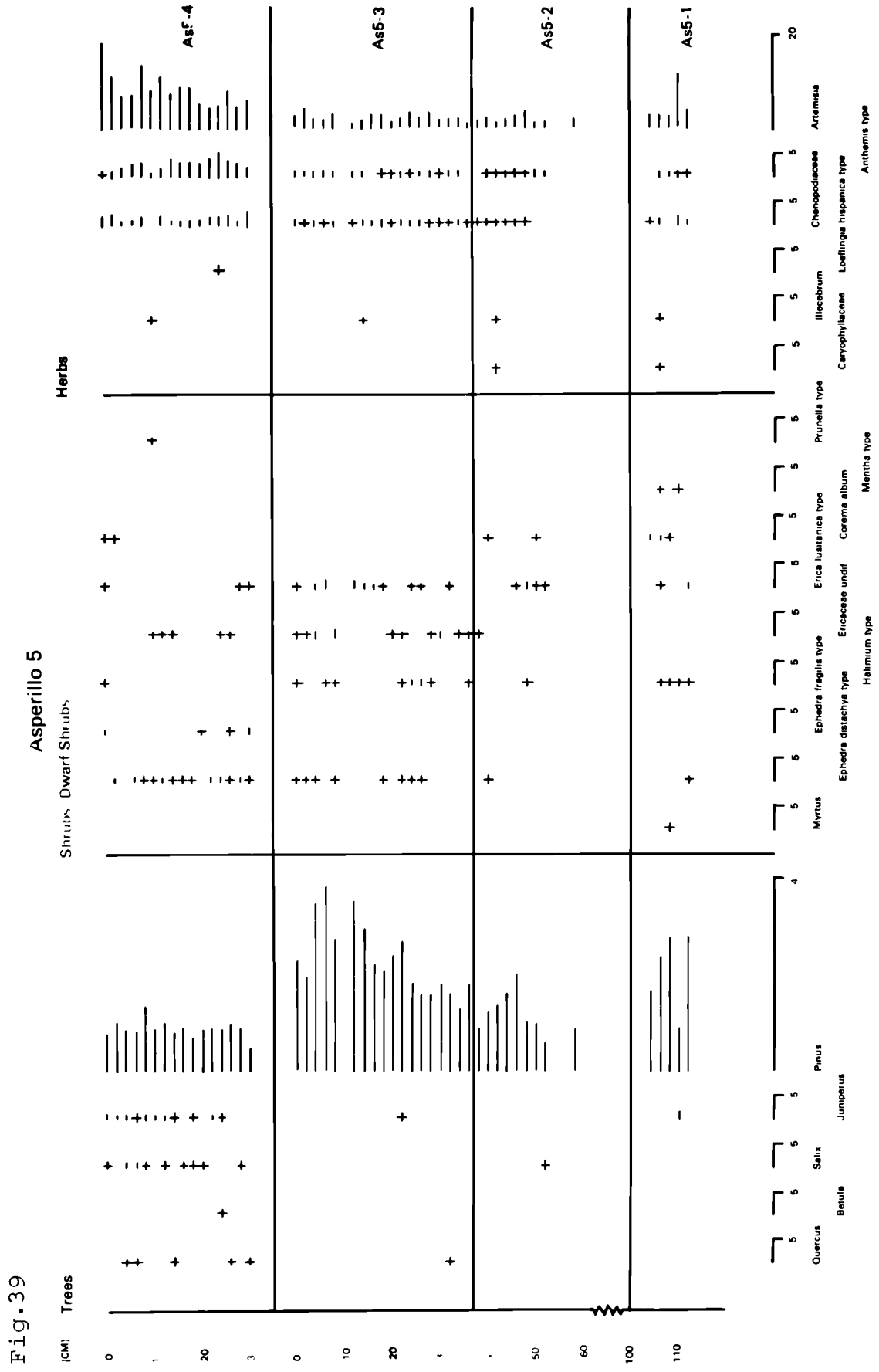

Asperillo 5
Trees
Shrubs Dwarf Shrubs
Herbs
(CM)
As5-4
As5-3
As5-2
As5-1
Quercus
Betula
Salix
Juniperus
Pinus
Myrtus
Ephedra distachya type
Ephedra fragilis type
Ericaceae undif
Erica lusitanica type
Halimium type
Corema album
Prunella type
Mentha type
Caryophyllaceae
Illecebrum
Chenopodiaceae
Loeflingia hispanica type
Artemisia
Anthemis type

Fig.39

Fig.40

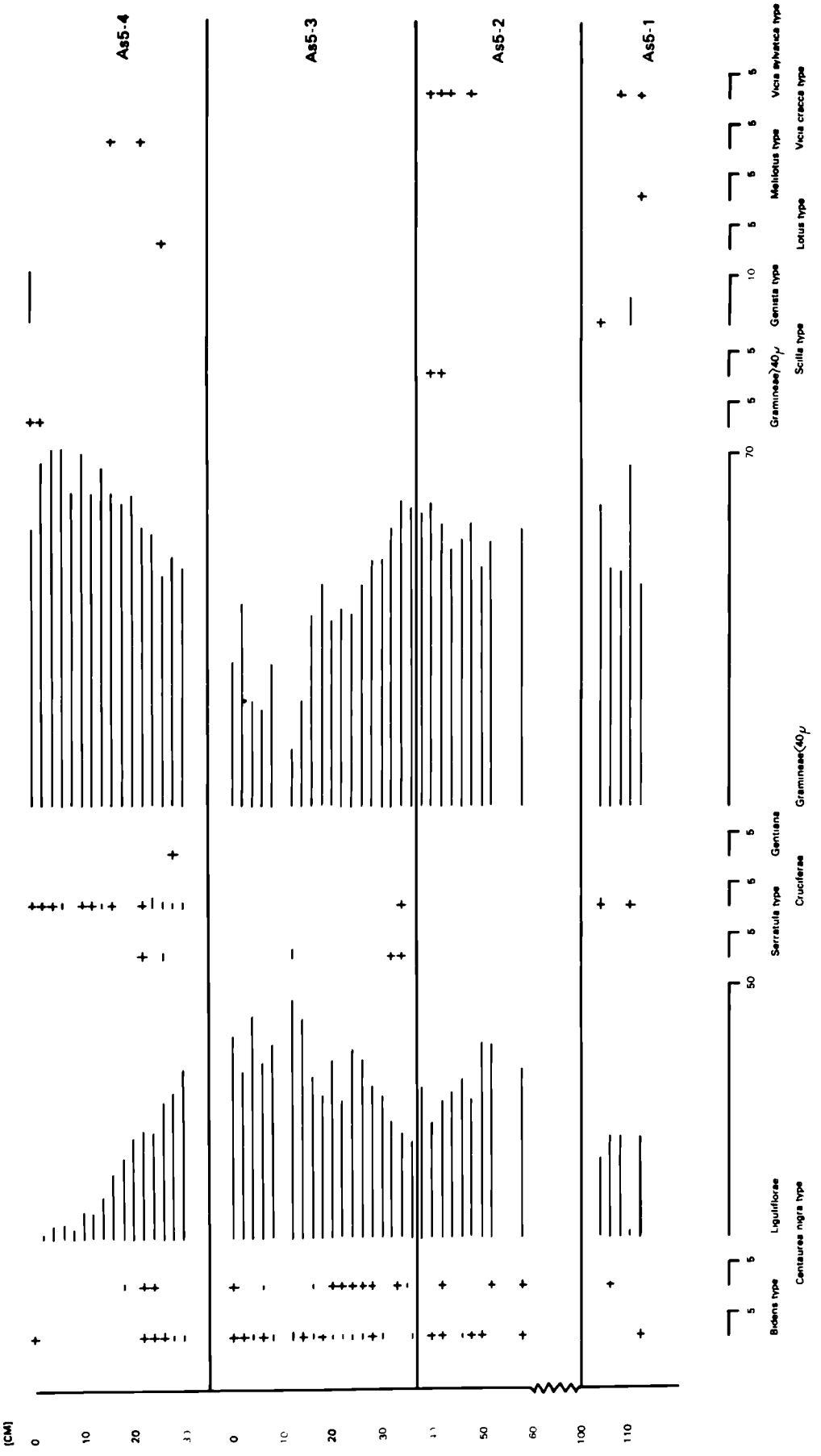
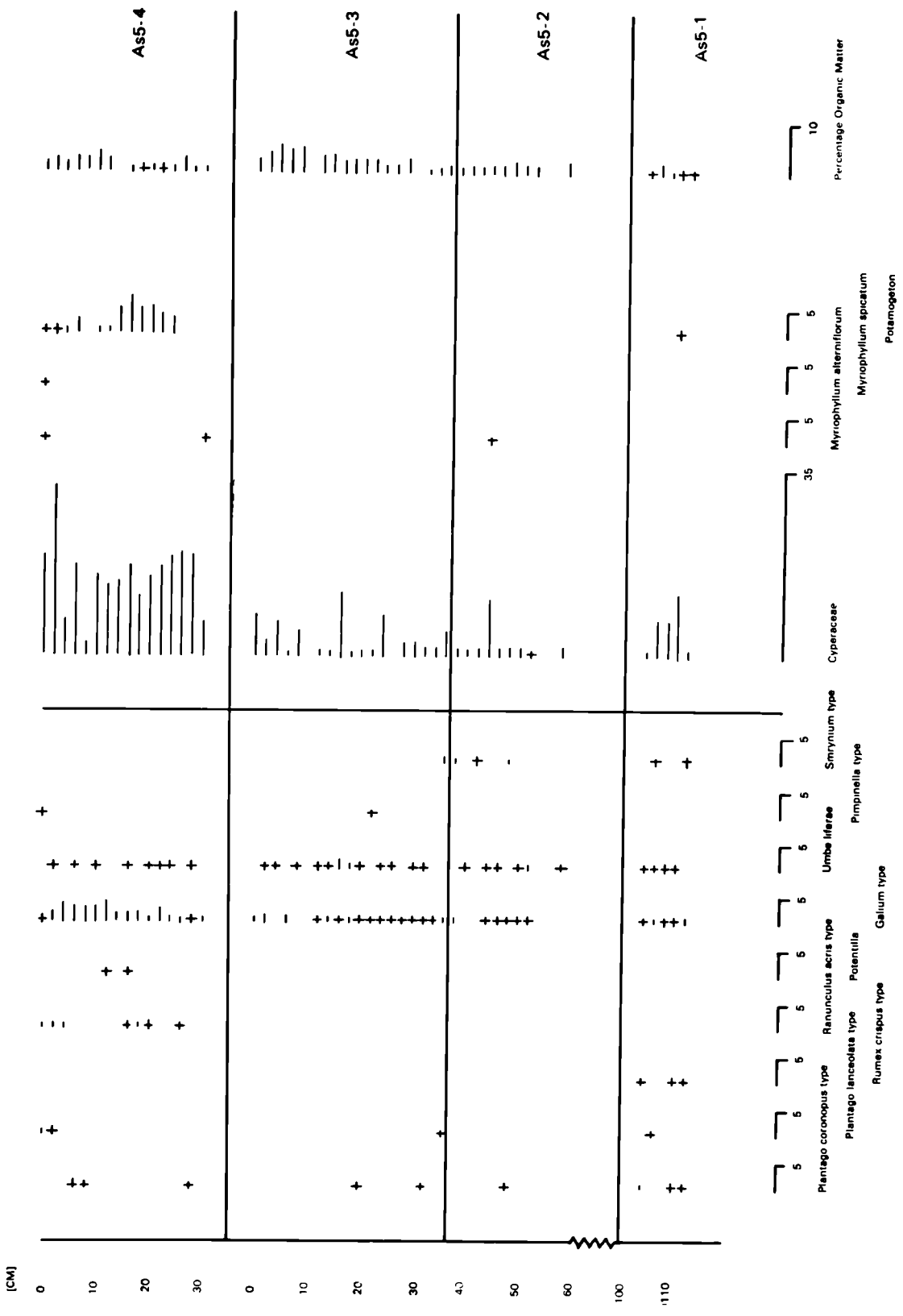

Asperillo 5
As5-4
As5-3
As5-2
As5-1
(CM)
0
10
20
30
50
60
100
110
Bidens type
Liguliflorae
Centaurea nigra type
Serratula type
Gentiana
Cruciferae
Gramineae<40μ
Gramineae>40μ
Scilla type
Genista type
Lotus type
Melilotus type
Vicia sylvatica type
Vicia cracca type

Fig.41


Asperillo 5
As5-4
As5-3
As5-2
As5-1
(CM)
0
10
20
30
0
10
20
30
40
50
60
100
110
Plantago coronopus type
Plantago lanceolata type
Rumex crispus type
Ranunculus acris type
Potentilla
Galium type
Umbe liferae
Pimpinella type
Smyrnium type
Cyperaceae
Myriophyllum alterniflorum
Myriophyllum spicatum
Potamogeton
Percentage Organic Matter

Asperillo 5

This site situated GR105025 was observed to possess two distinct peat bands. The pollen diagram (Figs.39-41) contain both of these bands, the stratigraphy is given in Fig.38. The first peat band consists of zones As5-; -As5-3, As5-4 represents the second peat band. The first band had a non-polleniferous zone running from 60-102cm. Basis for zonation is given in Table 12.

Pollen Assemblage Zone As5-1

Conditions in this zone are very similar to those seen in the other pollen diagrams. Values of *Pinus* indicate the presence of a forest, the soils being generally dry, especially when compared to the second peat band of this sequence, with low amounts of *Artemisia* and Cyperaceae and high Liguliflorae and Gramineae. No development of monte negro hygrophytic shrub vegetation takes place during this zone since only low amounts of *Erica lustitanica* type pollen is found throughout. The high amount of *Genista* type pollen recovered from one of the levels of this zone is unusual in that this type was found to be seriously under-represented in the modern pollen study, thus the high values may indicate the existance of a large population of *Genista anglica*, *Stauracanthus genistioides* or *Ulex minor*, these types being characteristic of monte negro/monte blanco shrub, and is consistent with the absence of *Erica* pollen.

Pollen Assemblage Zone As5-2

The *Pinus* values in this zone rise and then fall, but are

lower than those seen As5-1. The gap in pollen representation could have been caused by destabilization of the sands leading to Pinus having to re-invade when conditions had stabilized once more. Gramineae values are still very high during the zone and increase throughout. Liguliflorae values decline although they are still high, which may indicate that the conditions in the slack still had not stablized since high Gramineae and high Liguliflorae figures are often found in unstable conditions. Artemisia is not prominent and indicates the lack of moist areas in this part of the slack.

Pollen Assemblage Zone As5-3

Pinus now increases very strongly in this zone, indicating sufficient stabilization of the sands has occurred allowing Pinus to expand; Liguliflorae values also increase to high levels, while Gramineae levels fall, which is consistent with increased stabilization of the sands and decreased cover due to shading, but this does not explain the Liguliflorae increase. Pinus falls once again at the end of the zone and this probably represents the onset on the next dune front. Extensive flooding does not appear to have occurred during this band as seen in previous diagrams and in the second peat band of this sequence.

Ephedra distachya type pollen input is again constant, but constant inputs of Betula, Quercus and Juniperus are not seen in this band as has been seen in other Asperillo sites.

Asperillo 5:- Second Peat Band

Pollen Assemblage Zone As5-4

Gramineae values are very high during this zone and increase in it. Liguliflorae values fall very steeply, probably due to the eradication of e.g. *Hypochaeris* as the site becomes flooded, which is very extensive in this zone with a permanent peak in *Potamogeton* which is not found in modern day slacks, and high values of *Artemisia* and Cyperaceae indicating the existence of extensive wet conditions, which are probably the cause of the low *Pinus* values during this zone.

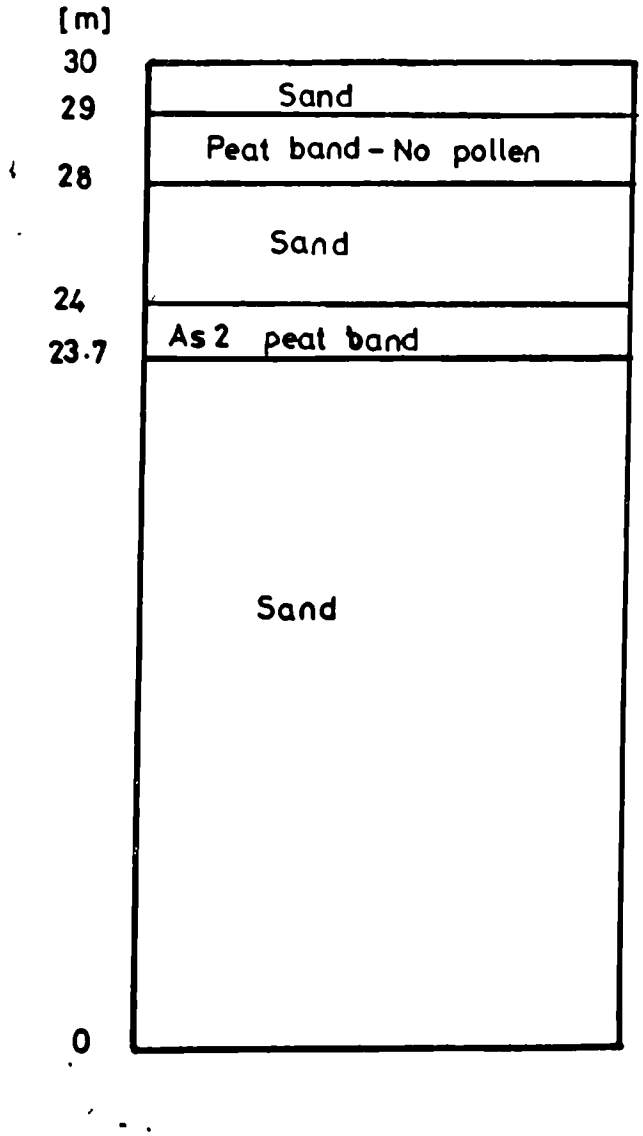
TABLE 13

ASPERILLO 2

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
As2-3	*Pinus*-Cyperaceae	*Pinus* high, Cyperaceae high, Gramineae low.
As2-2	*Pinus*-*Salix*	*Pinus* increase, *Betula*, *Alnus*, *Salix* all high. Cyperaceae increase.
As2-1	*Pinus*	*Pinus* high

Fig.42

Asperillo 2 - Stratigraphy



Asperillo 2

Fig.43

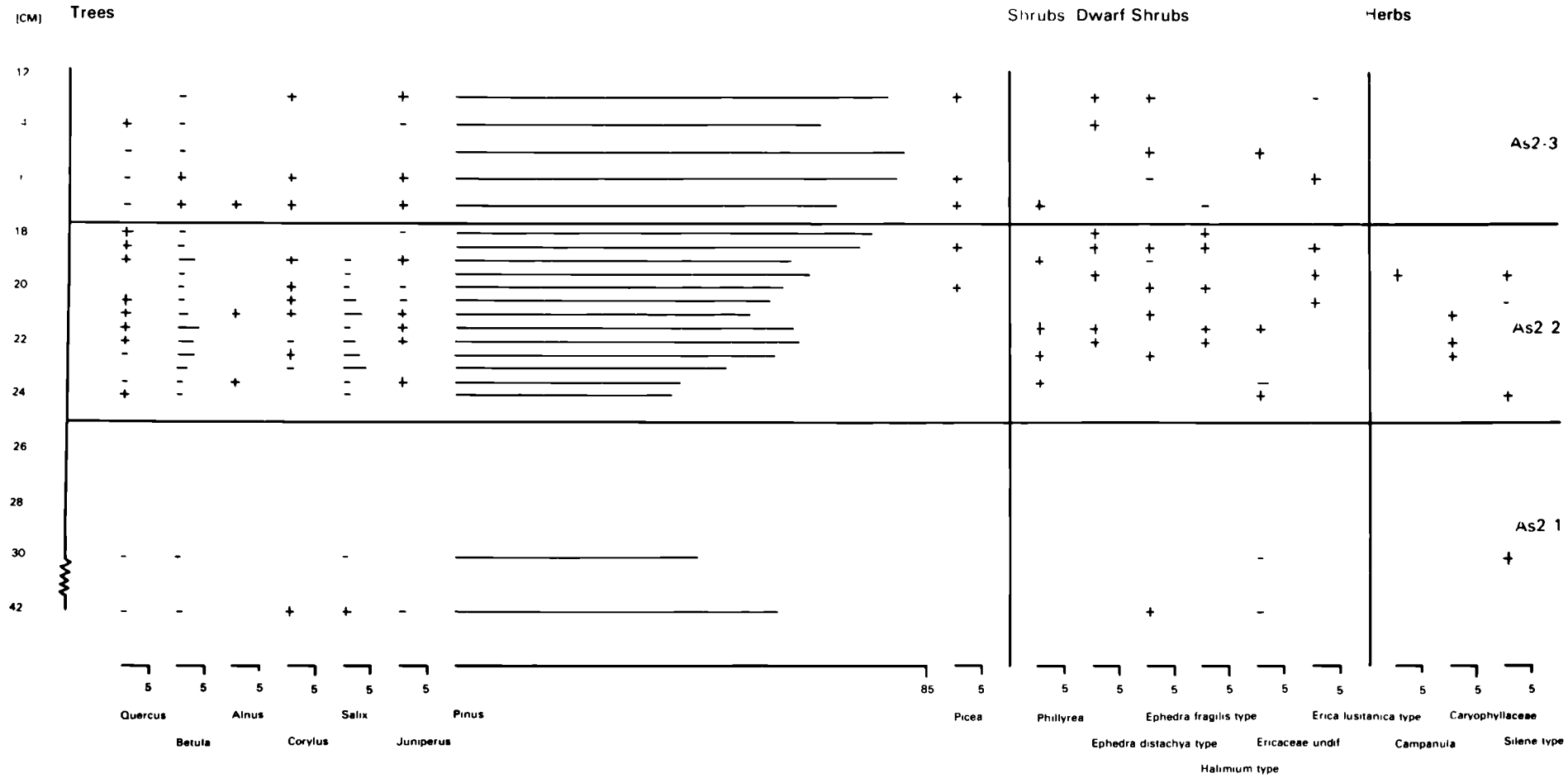
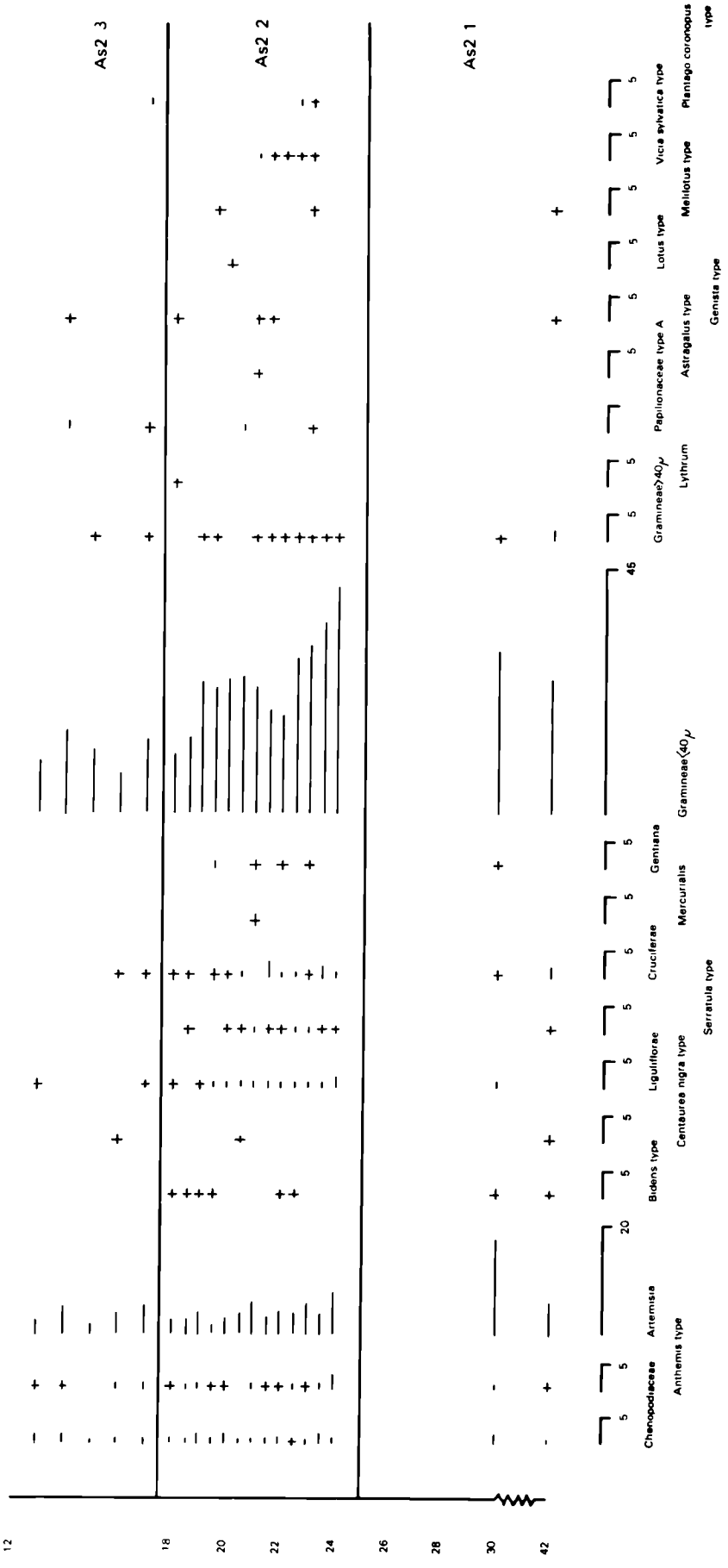


Fig.44

Asperillo 2



Asperillo 2

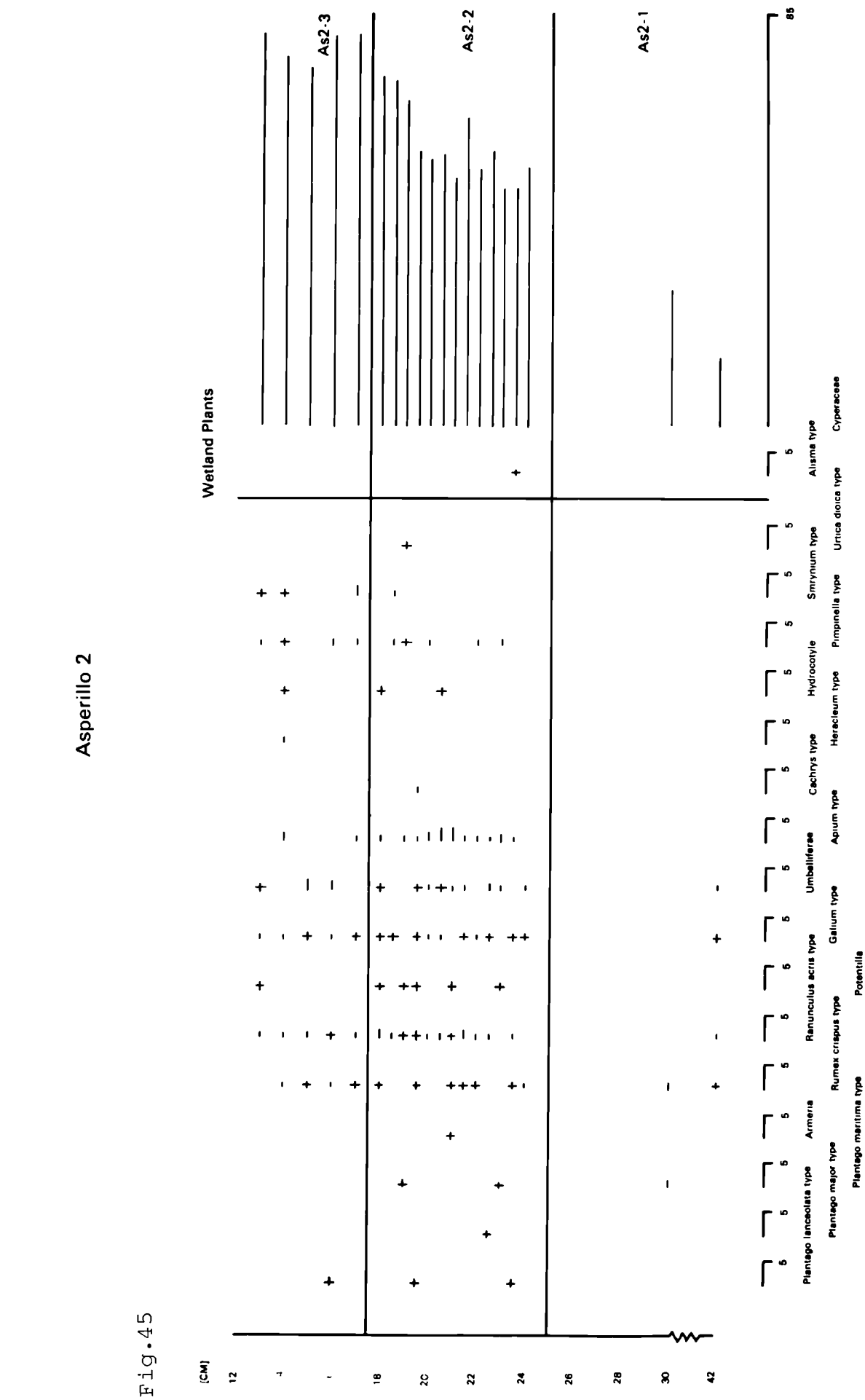
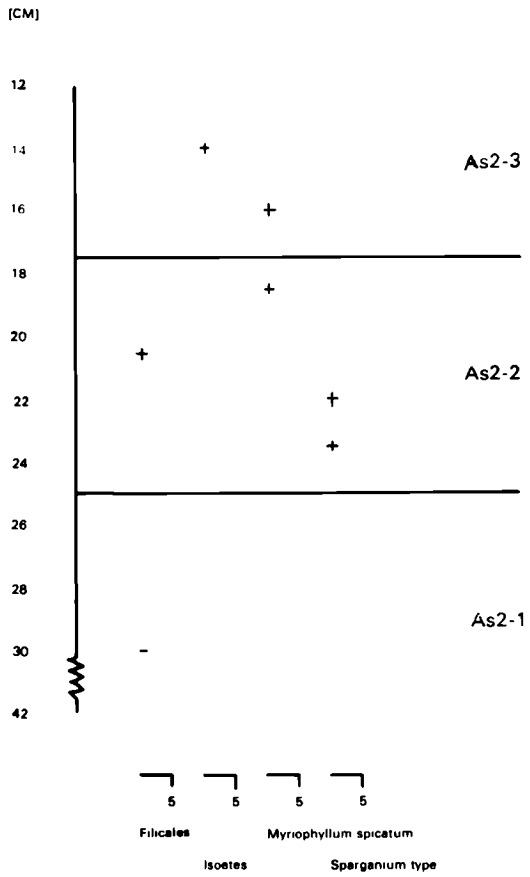


Fig.45

Fig.46

Asperillo 2



Asperillo 2

This site situated at G R 080040 consisted of two bands, but the upper one proved to be sterile (Fig.42). The pollen diagram of the lower band is shown in Figs.43-46. No pollen was found in levels 24,28,32-40 and then above 13 (Basis for zonation is given in Table 13).

Pollen Assemblage Zone As2-1

This zone is characterised by high Pinus values suggesting extensive Pinus forest. Artemisia is also high which is unusual since the two types normally have an inverse relationship, but little can be said about the relationship of this zone to the rest of the core due to the hiatus.

Pollen Assemblage Zone As2-2

This zone also has increasing Pinus (percentages are higher than have been found in any of the other sites or in the modern day pollen survey), while Gramineae are decreasing. Artemisia values are also lower than the previous zone. A dense Pinus forest can be postulated for this zone, the Gramineae decreasing due to a shading effect of the Pinus canopy. Cyperaceae values are also high, which could be indicative of large populations of Carex arenaria or Holoschoenus vulgaris. The input of Betula, Salix and Corylus is very high, a feature that is discussed later in the chapter.

Pollen Assemblage Zone As5-3

This zone maintains the high level of Pinus observed from any diagram seen so far; the Gramineae values decrease even

further. Thus the maintenance of the conditions seen in the previous zone is continued here.

The sequence is then terminated by the erosion of the band.

Asperillo:- General Discussion

The pollen diagrams from the peat bands at Asperillo all show great similarity to one another. As3 is the more complete of the bands and shows most of the vegetation succession, whereas other bands represent only portions of the main sequence.

Common features of the bands include:-

i) Large amounts of Liguliflorae pollen early in the band

ii) Flooding evidence at the termination of most bands

iii) Long distance pollen input

i) Liguliflorae component

The large amount of Liguliflorae pollen received from early on in the development of the peat band, before the onset of full *Pinus* forest is striking. Obviously members of the Liguliflorae are well adapted to the early successional phases of dune slack development when conditions are still unstable. With the onset of full *Pinus* forest than a shading effect probably is responsible for the removal of these early pioneers. This situation is in contrast to the modern day pollen rain of these communities for little Liguliflorae pollen is recovered from them, and members of the Liguliflorae are not recorded from the early successional phases as being of importance. Plants that are recorded as being of importance in these early stages today are plants like *Armeria pungens*, *Artemisia campestris*, *Carex arenaria*, *Scrophularia frutescens*, *Agrostis stolonifera* and *Rumex tingitanus* (Fig. 47)

Of these Armeria and Scrophularia are rarely found in fossil pollen due to under-representation. Of these species, Artemisia pollen peaks are recorded from the later stages in the succession of the Asperillo peat bands, but modern day sites record it from the early successional phases (Torres Martinez et al 1976)

The representation of monte blanco/monte negro/monte negro hygrophytic shrub communities is also low in the fossil sequences. The later stages in the modern day slacks have extensive populations of these shrub systems, the type dependent on the depth of the water table (Fig.47), but as can be seen from the fossil Asperillo diagrams the amounts of Halimium type and Erica lusitanica type pollen are generally low throughout (Fig.48). Occasionally, e.g. As3 and As4 peaks of these types do occur but are seen to collapse as quickly as they occurred, and the indications are that these peaks were a response to fire in the slacks resulting in an improved temporary nutrient availability. Thus the shrub systems do not appear to have been as important in slack vegetation of the past as they are today.

ii) Terminal Flooding

Another common feature of the Asperillo diagram, is the characteristic flooding of the slack at the end of most cycles, i.e. As5-4, As4-3, As4-7, this effect was not apparent in As3. The flooding is associated with the approach of the next mobile dune, a feature found in the modern day slacks of the Doñana National Park (G. Novo 1979). However, the vegetation of the flooding episodes is markedly different from that found at present. The modern day slacks become

dominated by Echinodorus ranunculoides, Glyceria distans, Hydrocotyle vulgaris, Carex sp. Ranunculus baudotii and have a shrub development of Juncus sp. (Fig. 47). The fossil sites, however, develop vegetation characteristic of even wetter conditions, e.g. Myriophyllum alterniflorum, frequently occurs, together with Potamogeton in As5-4. Typha/Sparganium species may have formed the equivalent of the Juncus shrub community that occurs in the modern day slacks, however, it is possible that Juncus pollen would not be picked up from the fossil cores, for its pollen grains are readily degraded (Faegri and Iversen 1964) and do not survive in fossil form. The development of this wetter variant vegetation system therefore, implies a higher water table than in the present day slacks.

Evidence that the slacks have been more stable in the fossil diagrams than those of today comes from the Juniperus pollen values, which tend to rise at the end of the bands especially As4-3, As4-7. It must be remembered that the pollen rain of Juniperus can be under-represented, which means that the values of Juniperus at the end of As4-3 and As4-7 indicate the development of Juniperus forest. Juniperus normally replaces Pinus in Mediterranean regions if conditions are stable enough (Harrant and Jarry 1967), and in the Donana sites this tends to happen after 40 years (G. Novo 1979).

Further evidence of stability of these slacks comes from the Salix inputs in As4-3 and As4-7 in association with the flooding episodes, but while the input of Salix pollen could derive from outside of the slack system, it is probable that

Fig.47 DUNE/DUNE SLACK CYCLES IN DOÑANA NATIONAL PARK AFTER Allier et al 1974

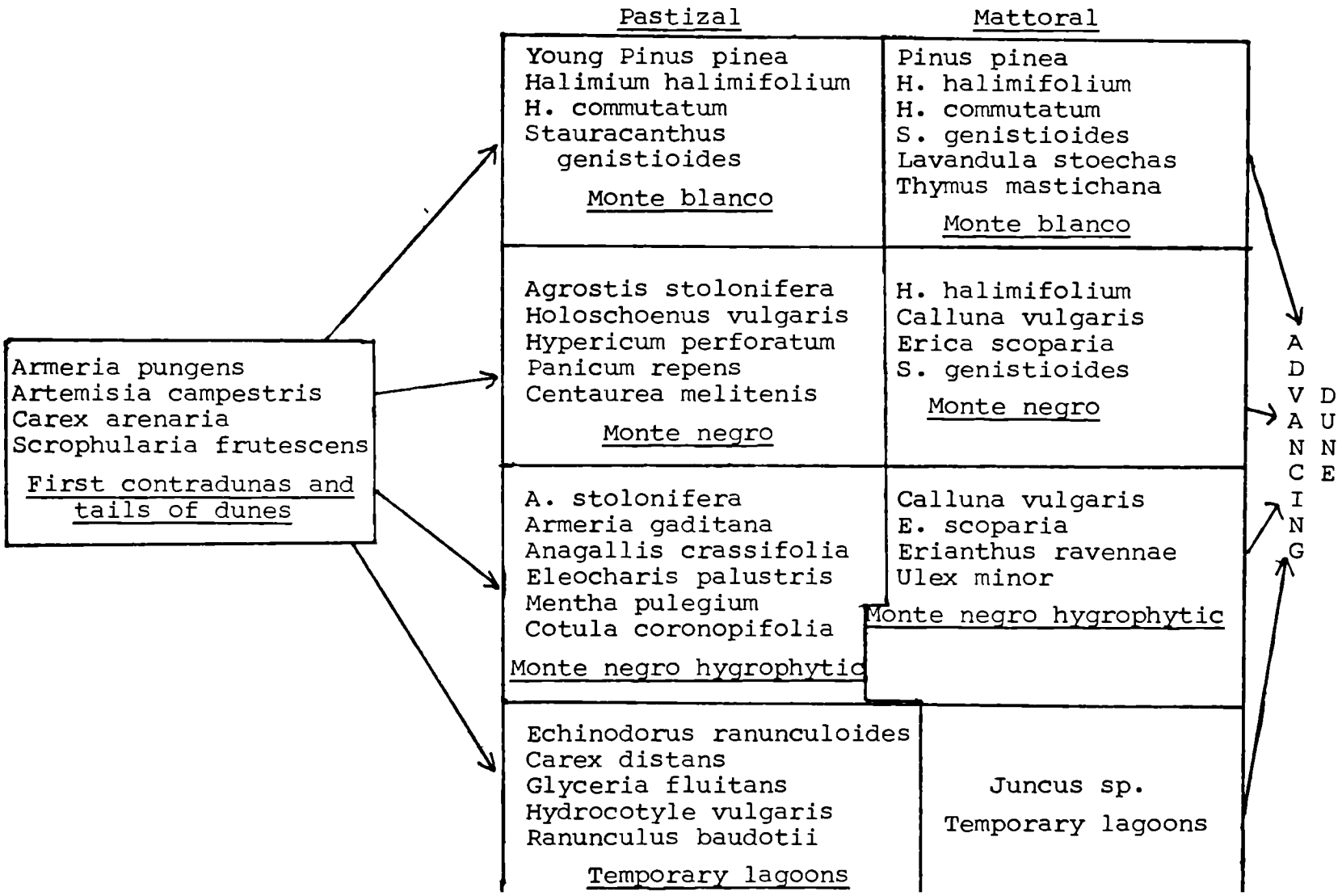
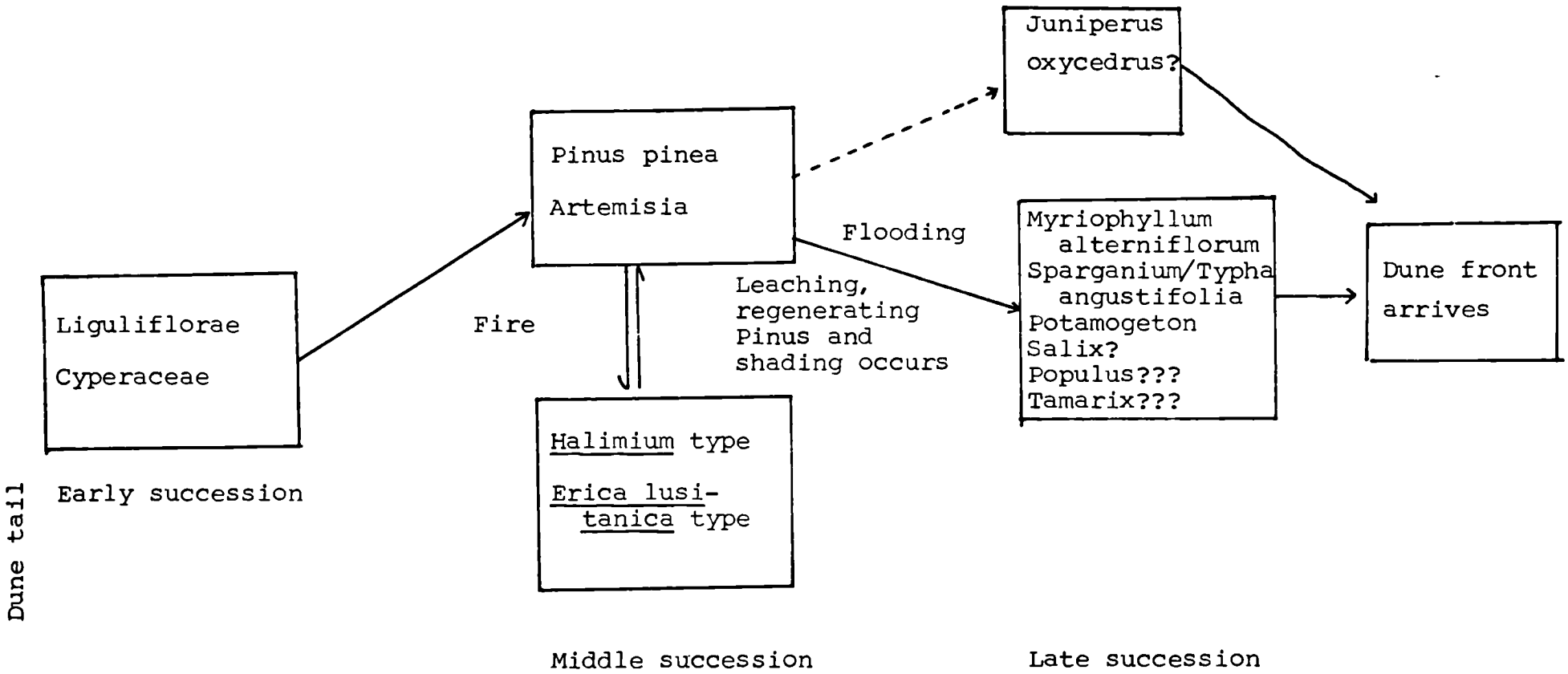


Fig.48 POPULATED DUNE/DUNE SLACK CYCLE IN ASPERILLO PEAT BAND



the tree could find an ideal habitat around the lagoons. Nowadays Salix is not recorded from the mobile sand dune systems.

If conditions were more stable in the fossil dune slacks than today, then it is possible that the sites would have been invaded by Tamarix and Populus. Isolated trees of these two genera are found today, associated with scattered trees of Juniperus oxycedrus, over the mobile dune systems of the Doñana National Park. It is thought that these represent the remnants of a once extensive forest that inhabited the dune area when conditions were a lot more stable then they were today, Tamarix and Populus being associated with the drainage system of the site before the latest bout of mobile dune activity (G. Novo 1979). However, Populus and Tamarix are unlikely to be picked up in the fossil pollen record for two reasons:-

i) Populus is a tree,the pollen of which has been found to degrade very rapidly (Birks 1973)

ii) Tamarix, as has been shown from the modern pollen survey, is under-represented in the pollen rain.

iii) Regional Long-distance Pollen Input

A third feature of the fossil peat bands, is the regional component of the pollen input. Although the amount of this input is low, it allows one to make predictions about the forest types of S.W. Spain during this period. The pollen types that represent this regional input into the dune slacks are Quercus, Alnus, Betula, Corylus and Ephedra distachya

type, since all these species are not found associated with dune/dune slack sites today. The peat bands that contain appreciable inputs of the above genera are As4-1 - As4-3 and As2, of which As4 is notable for the constant input of Corylus and As2 for the large Betula input (3%). The input of Ephedra distachya type is low but a constant feature throughout all of the peat bands.

On examination of the regional pollen rain of the analogous modern day dune slack sites, we find that higher levels of Quercus, Corylus and Betula are much lower. The implication of these facts is that the forest types from which this input has derived must have been closer to the Doñana area than they are at present. The input of these trees demands the existence of a cooler, moister climate than at present. This cooler, humid forest of Alnus, Betula and Corylus is today restricted to deep gorges in the Sierra Morena, where the microclimate is suitable for such forest types. Thus it appears that a contraction of this forest vegetation has occurred and during the deposition of the Asperillo peat bands, it is of greater extent, perhaps being found on the Guadalquivir plain. The existence of a cooler, moist climate may explain the low input of Phillyrea found in the fossil sites compared to the modern day ones, for Phillyrea is a thermophilous forest species. The lower input of Quercus is puzzling however, for these are several Quercus species that are adapted to cool, moist conditions, i.e. Q. pubescens. The indications are therefore that Quercus may not have been as frequent as it is today.

A puzzling feature of the regional pollen input is that of Ephedra distachya type, for although the input is low, it is constant throughout most of the diagrams. Ephedra is a plant indicative of arid conditions and its presence would at first sight seem to contradict the existence of a cool moist forest. The constant input of Ephedra into the fossil sites is not shown in the modern day dune slack sites, thus indicating that Ephedra was of greater importance during this phase.

Assuming that the radio-carbon dates are reliable for the Asperillo peat bands, a date of 13,000 B.P. would put the deposition of the peat bands into the temporal equivalent of the late glacial of N. Europe. There is only one pollen core in S.W. Spain that goes back this far and this is from a lake near to Padul on the Sierra Nevada (Florschutz et al 1971) at an altitude of 1500m. The relevant part of the diagram that is temporally equivalent to the Asperillo site, revels a vegetation of Pinus, Artemisia, Chenopodiaceae and Ephedra. Quercus, which today forms extensive populations around the lake, was rarely recorded. Thus the vegetation at Padul during this time was of a steppic nature. The Pinus belt nowadays is found at an altitude 1000m higher than the lake at Padul, thus the vegetation belts of the Sierra Nevada were considerably lower than those of today, which supports the existence of a more extensive temperate forest on the Guadalquivir plain which is at or near sea level. The frequency of Ephedra during this phase of the Padul diagram is possibly the source of the Ephedra pollen input into Asperillo, for it is known that Ephedra pollen is

capable of travelling great distances (Maher,1964, Vinje and Vinje 1955).

The long distance input of Ephedra need not necessarily have derived from the Sierra Nevada. The species of Ephedra producing the pollen input into Asperillo must have been one of the Ephedra species that produces E. distachya type pollen; the Ephedra species which is recorded nowadays from the Sierra Nevada, and is presumably the species that expanded during the late glacial, is Ephedra fragilis and this produces a different pollen grain (this is the only type found in the modern pollen survey). Thus there must have been a major expansion of an Ephedra species that produces E. distachya type pollen during the time that the bands at Asperillo were being laid down. It is possible that the Ephedra pollen was from a different source area which had populations of Ephedra that produced E. distachya type pollen, such possible sources being the Atlas mountains of N. Africa. Strong southerly winds have been observed to blow for long periods near to Malaga (K. Webb, personal communication), bringing dust clouds from N. Africa. However, if N. Africa is the source of the Ephedra input, then this brings into question the Alnus, Betula and Corylus inputs, for of these only Alnus occurs in N. Africa. Therefore the case for the Atlas mountains as a source of Ephedra is diminished. The predominant winds of the Donana area today are south westerly, and these would have to pass over many thousands of miles of ocean and therefore would contain little long-distance pollen.

Identity of Pinus and Juniperus

There are three main species of Pinus that could be responsible for the dune slack populations in the fossil pollen diagrams from Asperillo, these are Pinus halepensis, P. pinaster and P. pinea. Of these P. halepensis is restricted to calcareous soils, which leaves P. pinaster and P. pinea as possible candidates. Both are trees of maritime sands. Examination of type material of both species has revealed that they both have the same size range in their pollen grains, although only three type slides are available for comparison. Differentiation on size may be possible, but a lot more type material would need to be examined. P. pinea is the tree involved in the present day Donana slacks while P. pinaster does not invade these slacks very readily. Thus P. pinea may well have been the tree responsible for the forests seen in the Asperillo diagrams.

The Juniperus input, can be narrowed down to two main species:- J. phoenicia and J. oxycedrus, of these two, J. oxycedrus is the more oceanic and with the evidence of moister conditions occurring during the deposition of the peat bands it is possible that J. oxycedrus was responsible for the pollen input found there.

CHAPTER FOUR

Laguna de las Madres

The site known as Laguna de las Madres del Avitor (hereafter known as Laguna de las Madres) is situated 13km west of Huelva beside the road between Huelva and Matalascañas GR 895143. Geologically the site is surrounded by Quarternary sands of aeolian origin and are the same sands that cover most of the Doñana area. To the north of Laguna de las Madres the underlying Pliocene sands are uncovered showing that the aeolian sands have reached their eastern limit near to the site (I.G.M.E.1975).

The site had been previously examined by Menendez Amor and Florschutz (1964), from which they extracted a core of 5.5m but thought that the peat thickness was over 15m but which they could not extract due to boring difficulties. The site nowadays has been heavily exploited for horticultural peat production, and the peat workings have revealed the peat base to be about 5.5m (I.G.M.E. 1976) below the old surface.

The origin of the site was a basin cut into the Pliocene sands from which a river flowed into the sea, the outflow being below present day sea level. The river was subsequently cut off by large quantities of aeolian sands (I.G.M.E.1976) probably of the same origin as the sands that cover the rest of the Donana area to the west, e.g. Asperillo dunes. Once the outflow has been blocked, water level began to rise and by a process of hydroseral succession peat initiation began

Despite the site having already been examined by Menendez Amor and Florschutz (1964) it was decided to further examine the site for the reasons given in Chapter 1.

The modern day vegetation of the site is dominated by Phragmites australis and surrounding the site are plantations of Pinus pinea (see modern pollen survey of vegetation for further detail). Cultivation of Fragaria ananassa also occurs adjacent to the site. The rest of the vegetation follows that described in the modern vegetation survey of the Doñana area, though only shrub communities were seen to exist in the immediate vicinity of the site.

Methods

Three cores were obtained from the site, two of which were taken from the S.W. end of the Laguna (Fig.10):- LM1 and LM2, LM1 was 2.60m in length and LM2 2.84m. A third site LM3 was analysed from near the bridge before the two rivers that flow into the Laguna diverge. This core was 2.86m long. All the cores were extracted using a Russian borer (Jowsey 1966) and transferred to 0.5m long plastic drainpipes, which were then transported back to London by air and subsequently stored in the dark at 2°C until required for analysis. Preparation of the samples follows the methods given in Appendix B. Samples were taken every 4cm in LM1 and LM2 and every 8cm in LM3. Duplicate slides were made up and 500 pollen excluding Cyperaceae, Aquatics and Filicales were counted from each slide if possible. In the lower regions of the core this proved not to be possible. Identification of pollen follows that of Moore and Webb (1978), for types not found here, refer to Appendix A where further details are given.

The pollen diagrams have been zoned conventionally and are given in Figs.49-67, the basis of zonation and stratigraphy is given in Tables 14-19. The pollen types have been grouped into broad life-form groupings:- Trees, Shrubs and Lianas, Dwarf shrubs, Herbs, Fern spores and Aquatics. The pollen types are expressed as follows:-

i) Tree, Shrub, Dwarf shrub and Herbs are all expressed as a percentage of the Total pollen - Cyperaceae, Aquatics and Filicales.

ii) The Aquatics and Filicales are expressed as a percentage of the Total pollen - Cyperaceae

iii) The Cyperaceae are expressed as a percentage of the Total pollen

TABLE 14

Laguna de las Madres 2:- Stratigraphy

Depth (cm)	Description
0-15	Unhumified *Phragmites* peat
15-50	Humified brown *Phragmites* peat
50-55	Blacker himified peat
55-90	Brown humified peat
90-100	" " " with mineral inwash
100-120	Brown humified peat
120-130	Darker black peat
130-150	Black peat
150-170	Brown peat
170-187	Black peat
187-200	Brown peat
200-208	Black peat
208-210	Fine clay
210-214	Grey sand/silt + plant remains
214-218	Fine clay
218-284	Sandy lake sediments

TABLE 15

LAGUNA DE LAS MADRES 2

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
LM2-8	*Quercus*-*Pinus*	*Juniperus*, *Pinus* fall, Gramineae rise
LM2-7	*Quercus*-*Pinus*-*Juniperus*	*Quercus* falls, *Juniperus* and *Pinus* rise, *Plantago* and *Rumex* peak
LM2-6	*Quercus*-*Salix*-*Pinus*	*Quercus* peak, *Salix* peak, *Pinus* rises, *Juniperus* low, *Plantago*/*Rumex* high
LM2-5	*Quercus*-*Juniperus*	*Quercus* falls, *Pinus* absent, *Juniperus* peak, *Plantago* and *Rumex* high.
LM2-4	*Quercus*-*Salix*-*Erica*	*Quercus* rise, *Salix* peak, Gramineae decreases. *Erica* peak
LM2-3	*Quercus*-*Pinus*-Gramineae	*Quercus*, *Pinus* rise, *Erica* peaks, Aquatics peak, Chenopod, Liguliflorae decline.
LM2-2	Liguliflorae-*Isoetes*	*Quercus*, *Pinus* low, Liguliflorae rise (45%), *Nuphur* peak.
LM2-1	*Quercus*-*Pinus*-Chenopod-*Isoetes*	*Quercus* peak, *Pinus* high 4-10% *Phillyrea* falls. Chenopod peaks, *Isoetes* peaks.

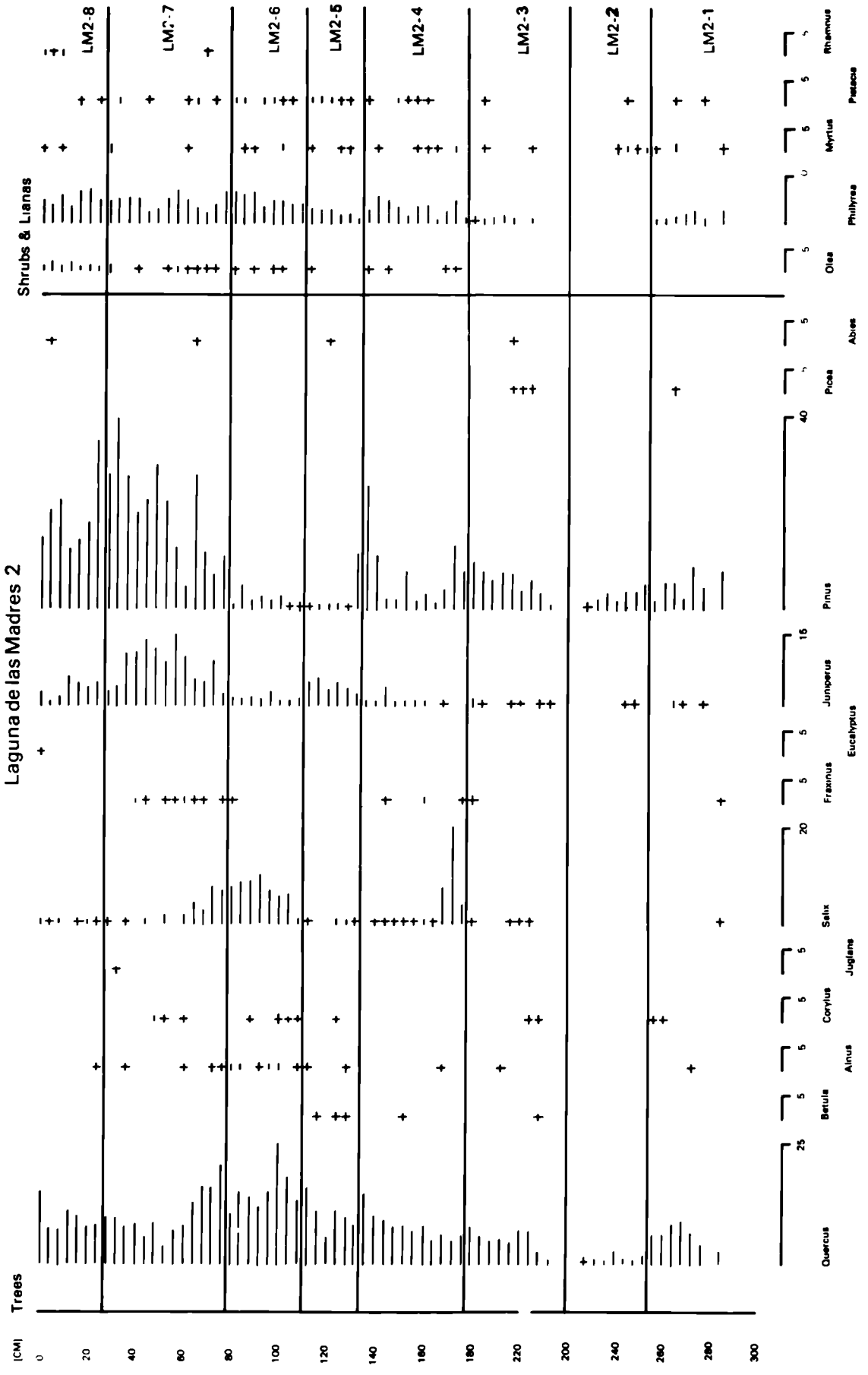

Laguna de las Madres 2
Trees
Shrubs & Lianas
(CM)
LM2-8
LM2-7
LM2-6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
Quercus
Betula
Alnus
Corylus
Juglans
Salix
Fraxinus
Eucalyptus
Juniperus
Pinus
Picea
Abies
Olea
Phillyrea
Myrtus
Pistacia
Rhamnus

Fig.49

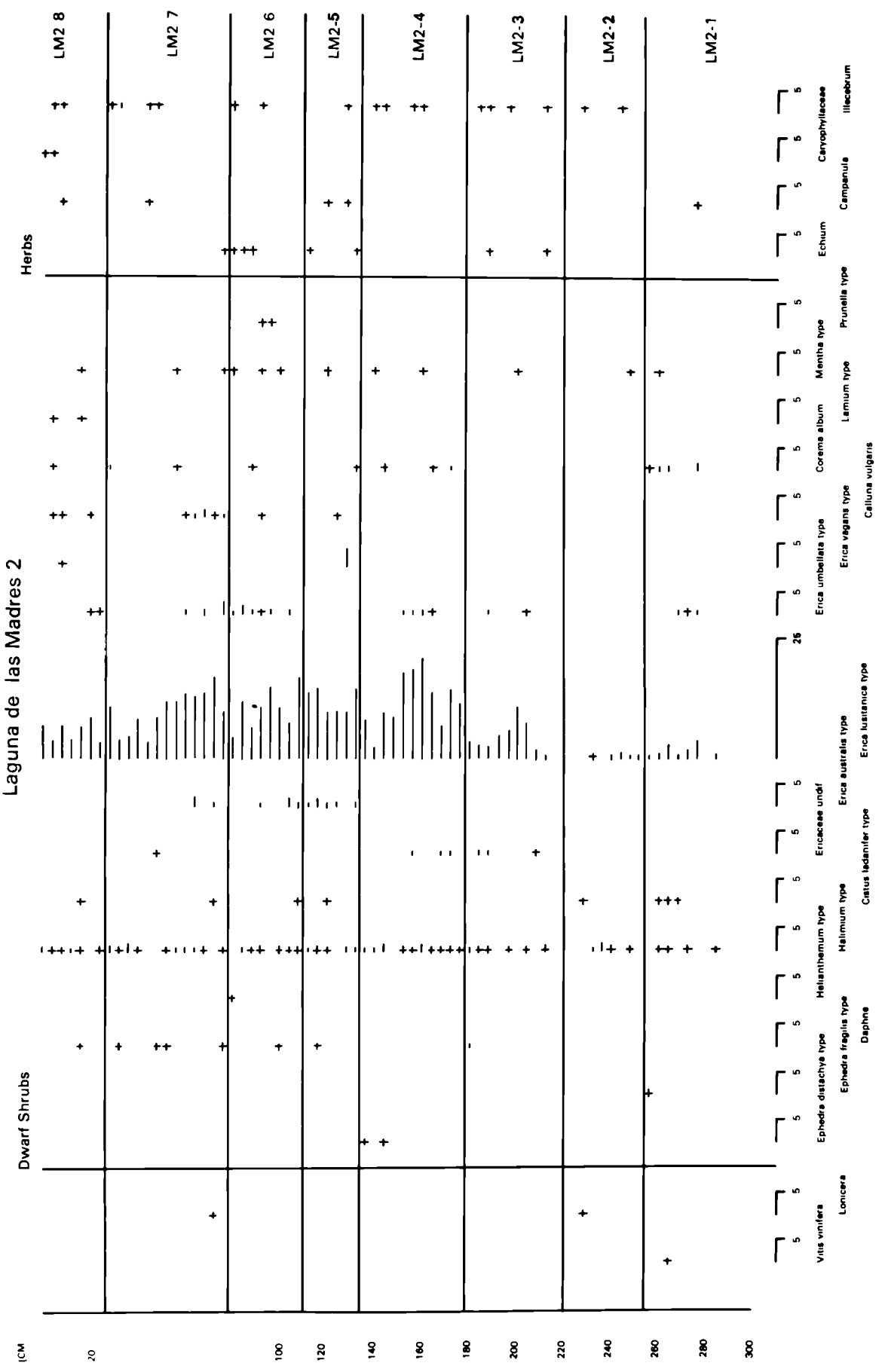

Laguna de las Madres 2
Dwarf Shrubs
Herbs
LM2 8
LM2 7
LM2 6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
CM
Vitis vinifera
Lonicera
Ephedra distachya type
Ephedra fragilis type
Daphne
Helianthemum type
Helimium type
Cistus ladanifer type
Ericaceae undif
Erica australis type
Erica lusitanica type
Erica umbellata type
Erica vagans type
Calluna vulgaris
Corema album
Lamium type
Mentha type
Prunella type
Echium
Campanula
Caryophyllaceae
Illecebrum

Fig.50

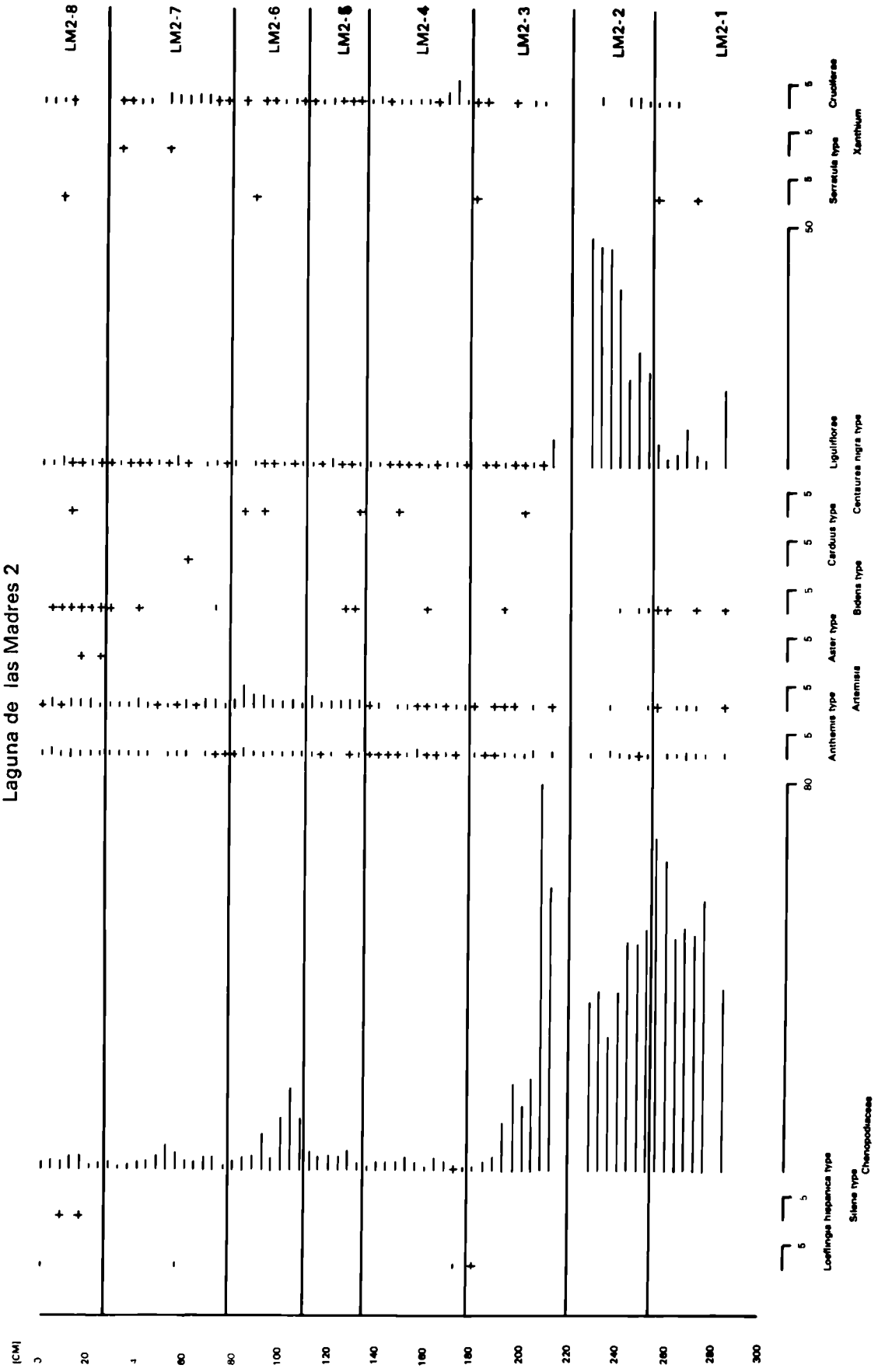

Laguna de las Madres 2
LM2-8
LM2-7
LM2-6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
(CM)
Loeflingia hispanica type
Silene type
Chenopodiaceae
Anthemis type
Artemisia
Aster type
Bidens type
Carduus type
Centaurea nigra type
Liguliflorae
Serratula type
Xanthium
Cruciferae

Fig.51

Fig.52

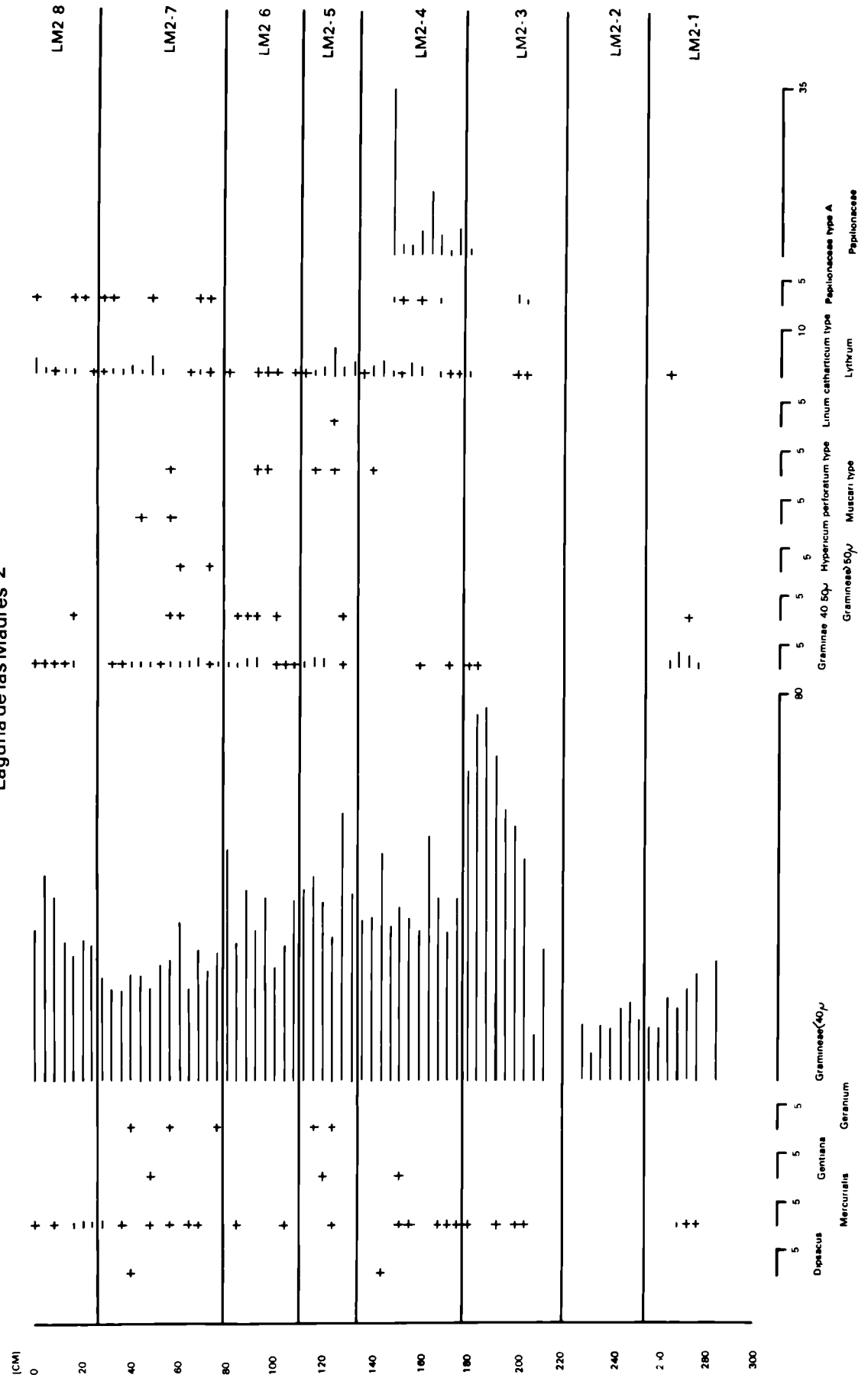

Laguna de las Madres 2
LM2 8
LM2-7
LM2 6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
(CM)
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
Dipsacus
Mercurialis
Gentiana
Geranium
Gramineae(40μ
Gramineae 40 50μ
Hypericum perforatum type
Gramineae 50μ
Muscari type
Linum catharticum type
Lythrum
Papilionaceae type A
Papilionaceae
Scilla type
5
10
35
80

Fig.53

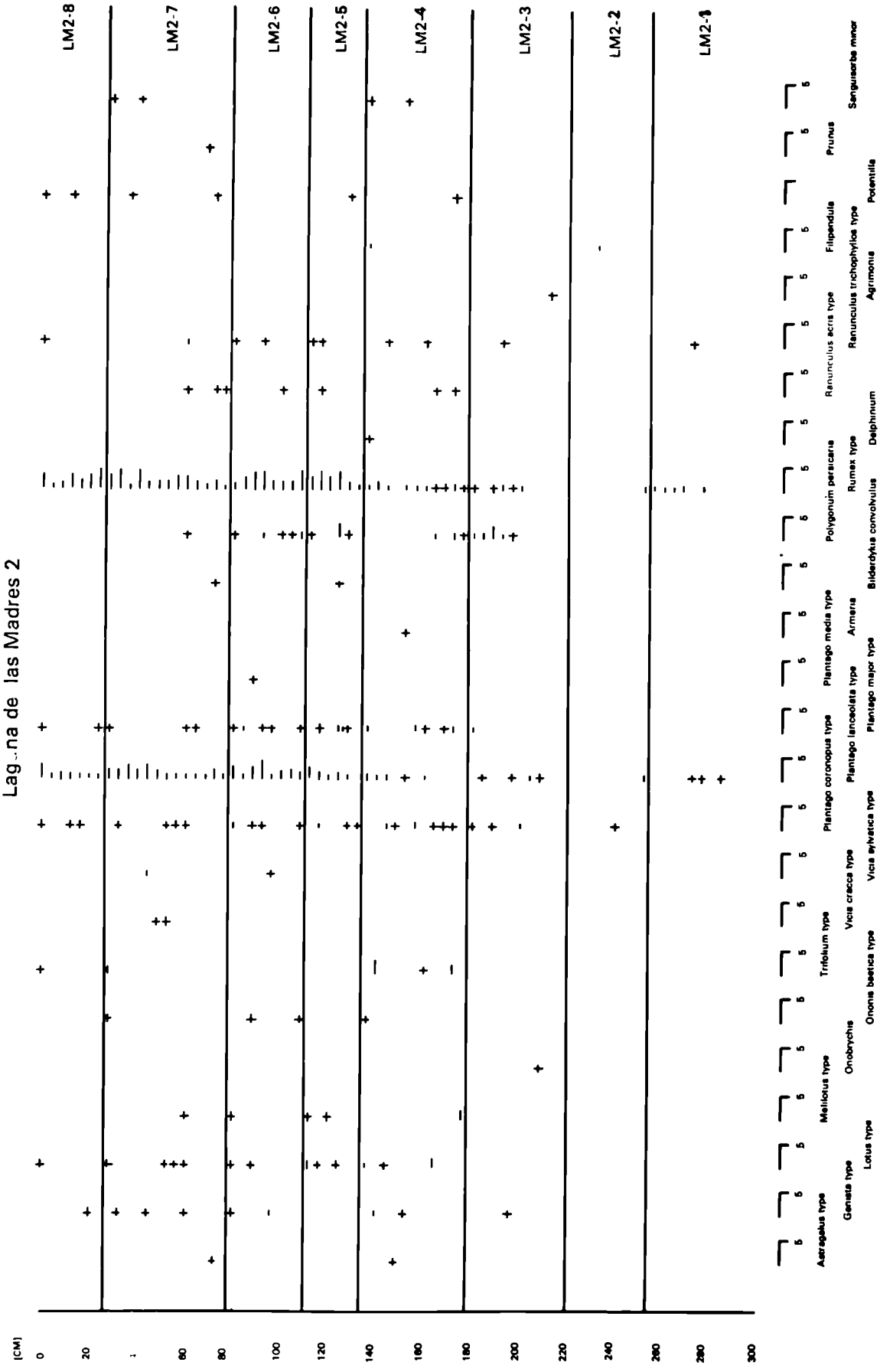
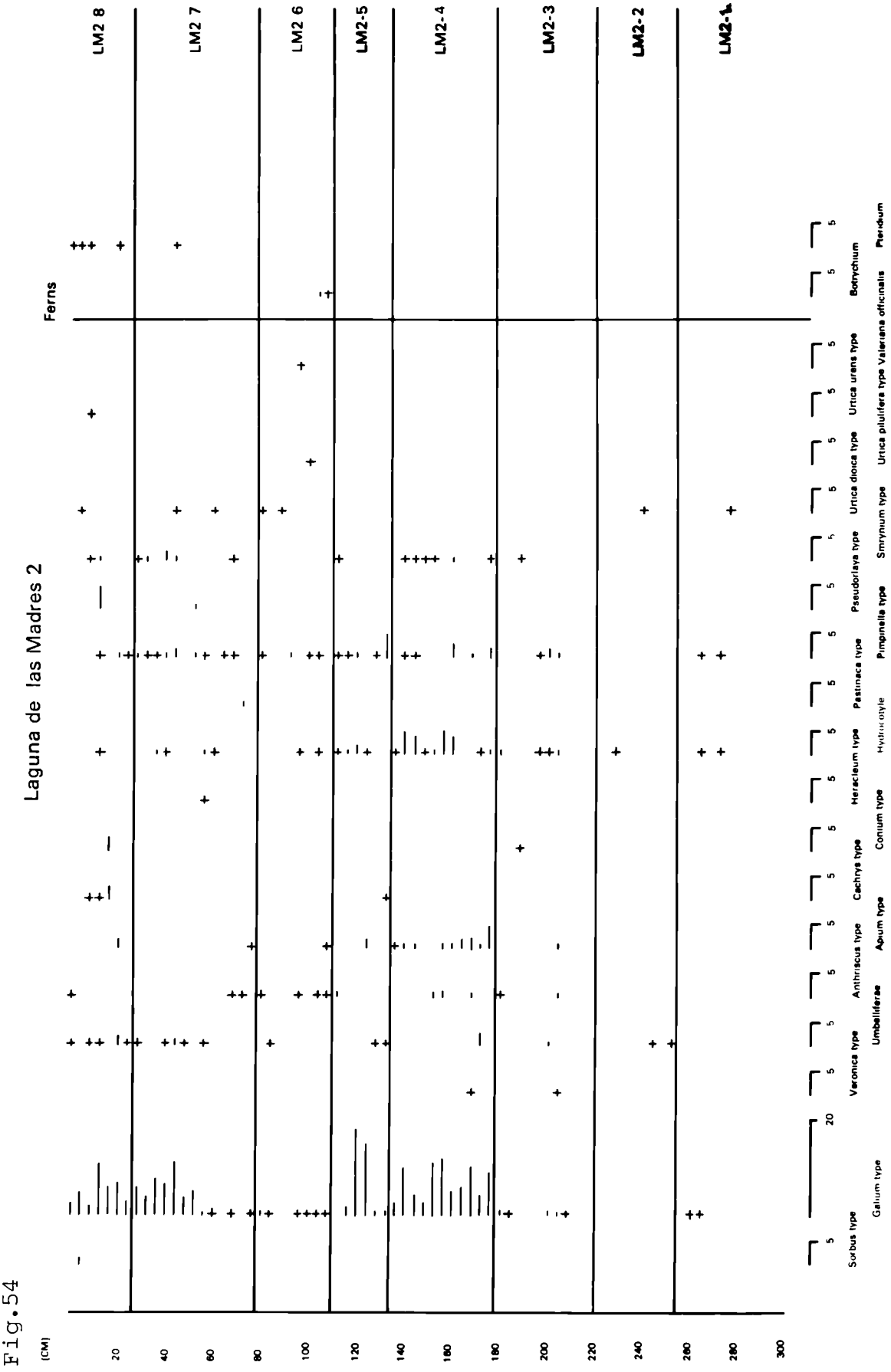

Laguna de las Madres 2
[CM]
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
LM2-8
LM2-7
LM2-6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
Asteraceae type
Lotus type
Genista type
Onobrychis
Ononis baetica type
Trifolium type
Vicia cracca type
Vicia sylvatica type
Plantago coronopus type
Plantago lanceolata type
Plantago major type
Plantago media type
Armeria
Bilderdykia convolvulus
Polygonum persicaria
Rumex type
Delphinium
Ranunculus acris type
Ranunculus trichophyllus type
Filipendula
Agrimonia
Prunus
Potentilla
Sanguisorba minor

Fig.54


Laguna de las Madres 2
(CM)
Ferns
LM2 8
LM2 7
LM2 6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
Sorbus type
Gahum type
Veronica type
Umbelliferae
Anthriscus type
Apium type
Cachrys type
Conium type
Heracleum type
Hydrocotyle
Pastinaca type
Pimpinella type
Pseudorlaya type
Smyrnium type
Urtica dioica type
Urtica pilulifera type
Urtica urens type
Valeriana officinalis
Botrychium
Pteridium

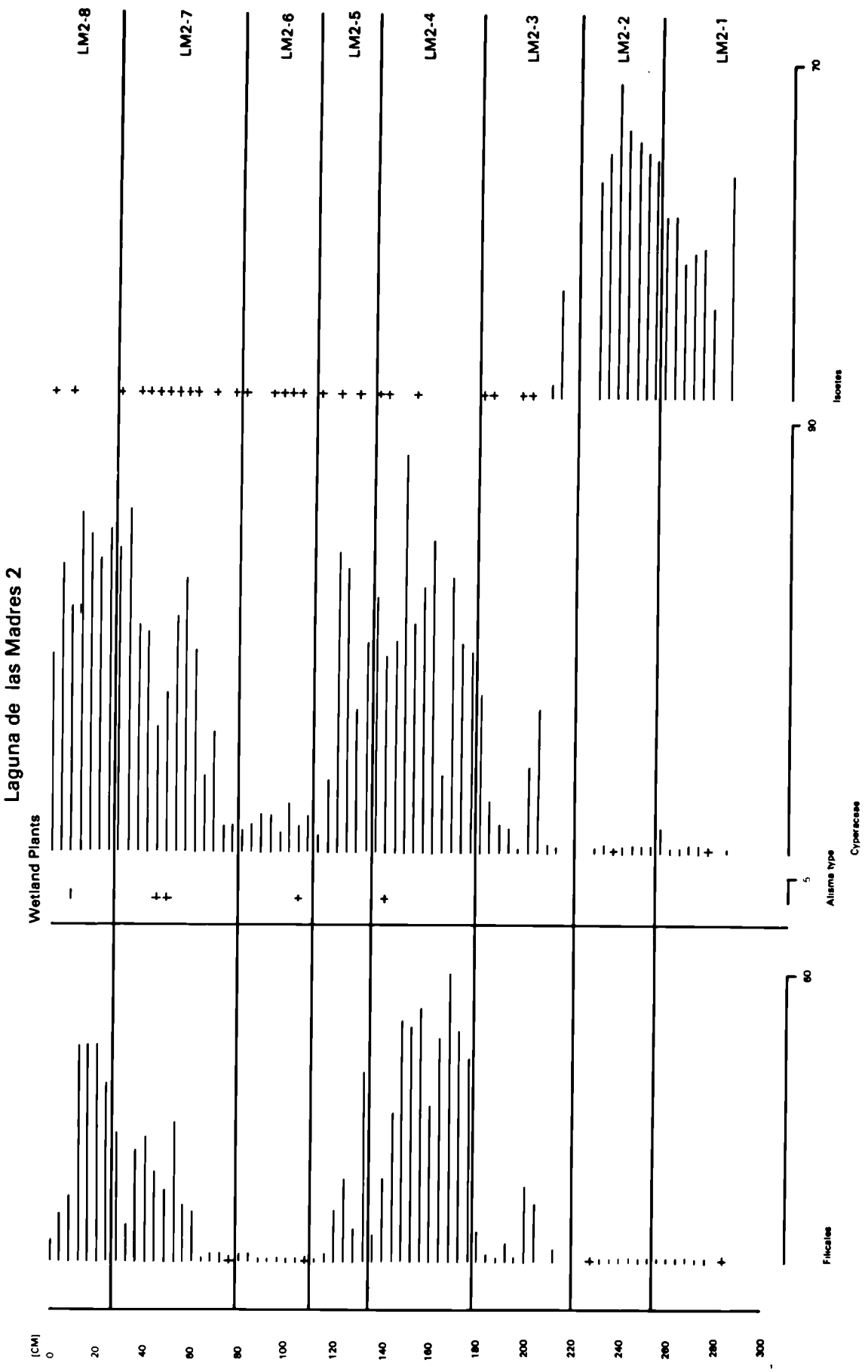

Laguna de las Madres 2
Wetland Plants
LM2-8
LM2-7
LM2-6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
[CM]
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
Fircales
60
Alisma type
5
Cyperaceae
90
Isoetes
70

Fig.55

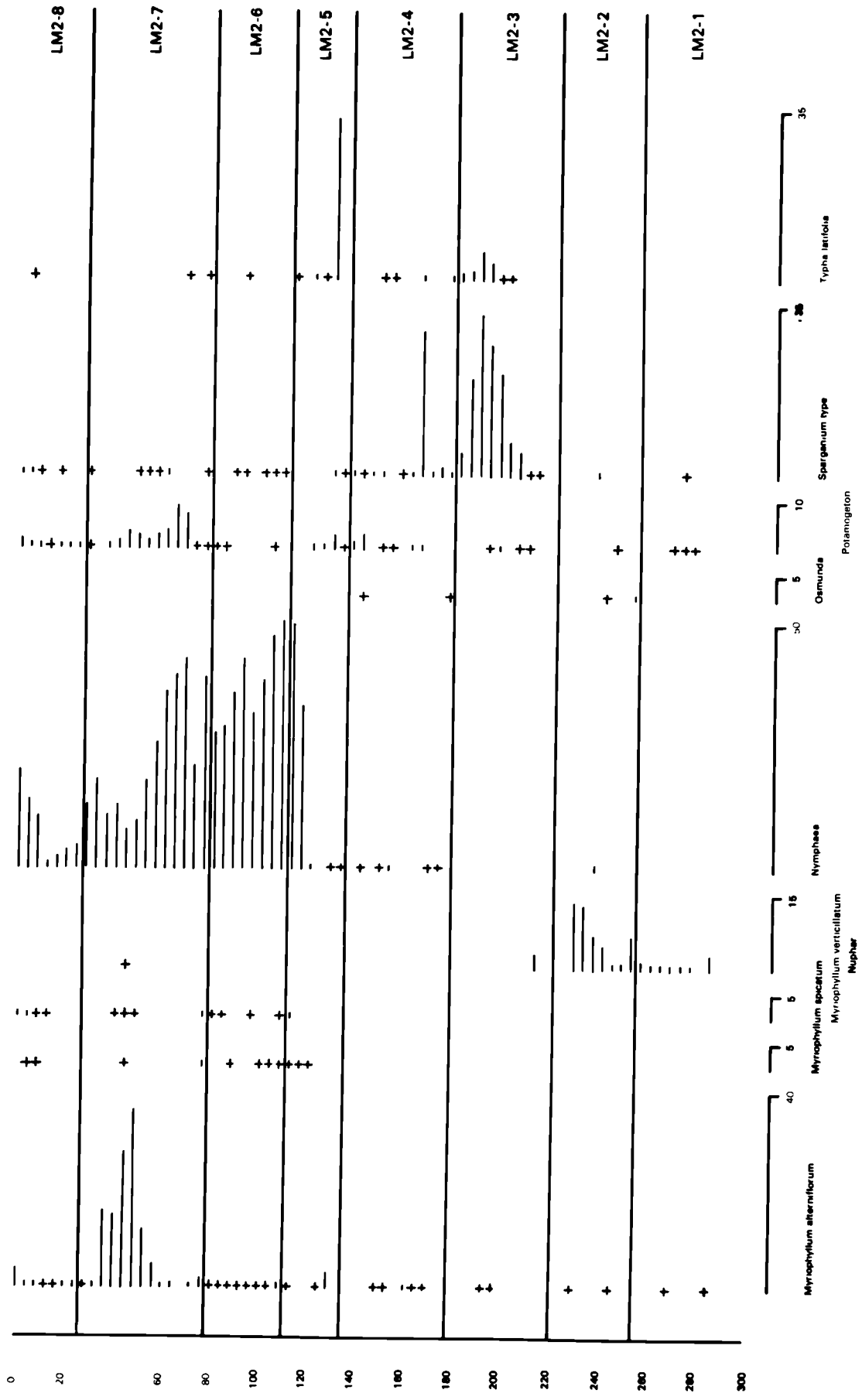

Laguna de las Madres 2
LM2-8
LM2-7
LM2-6
LM2-5
LM2-4
LM2-3
LM2-2
LM2-1
0
20
60
80
100
120
140
160
180
200
220
240
260
280
300
Myriophyllum alterniflorum
40
Myriophyllum spicatum
5
Myriophyllum verticillatum
5
Nuphar
15
Nymphaea
30
Osmunda
5
Potamogeton
10
Sparganium type
Typha latifolia
35

Fig.56

Laguna de las Madres:- Interpretation

Pollen Assemblage Zone LM2-1

Local

Locally the site was dominated by *Isoetes* and Chenopodiaceae at this time. The species of *Isoetes* responsible for the pollen input in this part of the diagram cannot be determined, though of the two modern day species found in the area, *I. velata* appears to be a more likely candidate, since it is a plant of shallow lake margins, whilst *I. hystrix* is a plant of sandy sites where water lies during the winter. The sediment suggests deposition under wet conditions and this would exclude *I. hystrix*, also *I. hystrix* does not produce at present great quantities of pollen in the ephemeral lagoons (surface samples D110). *Isoetes lacustris* is also a possible candidate, one would normally associate the presence of *Isoetes* as indicative of Oligotrophic conditions, however, the views of Seddon (1967) must be taken into account for he has observed a contraction of the ecological tolerance range of *I. lacustris* in Wales and suggests that *Isoetes* in the past could have inhabited eutrophic conditions. The absence of plants indicative of eutrophic conditions in this zone leads to the conclusion that the laguna was oligotrophic during this zone.

Associated with the peak in *Isoetes* is also a dominance of Chenopodiaceae and such high values are normally found only in sites where samples were taken from under pure stands of chenopods (N.E. Iran, this thesis part A). The sediments

of the site at this point are very sandy and suggest large amounts of inwash of sand from the surrounding area. The presence of high amounts of Chenopodiaceae pollen could indicate two possible types of environment:-

i) Brackish water - Salt marsh type of community

ii) Heavily disturbed/cultivated ground

Of the two, possibility i) does not correlate well with the Isoetes found, which is a plant of freshwater environments. The second possibility that the input is due to populations growing in disturbed ground could be true, for the soils of the area were disturbed during this period, which may be correlated with the action of mobile sand dunes and the chenopod pollen input derives from inwash of soils from these areas dominated by the family. An anthropogenic cause could also be postulated for evidence of cultivation does occur in this zone with the chenopods growing as weeds in the cultivated plots. A grain of Vitis was found, which may indicate viticulture, and a peak in Gramineae over 40μ is found, however, the high chenopod values are not recorded from LM3 where most evidence for viticulture occurs, therefore the grain of Vitis found may represent a natural population in the Mediterranean forests. One must also beware about correlating Gramineae >40μ with cereal cultivation for some wild Gramineae genera also produce large grains, e.g. Elymus and Glyceria (Beug 1961)

Regional

The regional forest at this time consists of Quercus, which increases and then falls. The species of Quercus involved

could be one of a number, some palynologists (e.g. Bottema 1974) have differentiated the genus Quercus into evergreen and deciduous types on the basis of pollen, but in the current investigation, the variation on many of the type slides of Quercus species was found to be wider than the supposed differences between the two groups and Beug (1967) comments that the differences between Q. suber and the deciduous Quercus species is not strong, although that between Q. ilex and them is. Since the vegetation at this time resembles that of a Mediterranean type community on comparison with the modern pollen rain, one can make certain assumptions concerning the species of Quercus involved. One Quercus that is thought to have formed extensive forests but is only present in small populations today is Q. suber, but the possibility exists that some of the present trees of the area have been planted (Chapter 5). Other candidates are Q. rotundifolia which occurs on the more calcareous soils and which is replaced by Q. suber on the acidic silicious soils. Q. coccifera a plant of the shrub vegetation, of which a few plants have been found today in the Donana area (G. Novo 1979), but it is not known to what extent this plant was important in the past. Q. faginea agg. a tree that is very rare in Spain was once thought to have formed extensive forests over most of the Doñana area (G. Novo, personal communication). However, of all the species it is likely that Q. suber and Q. rotundifolia were the major forest formers of the area..

Associated with the Quercus forest are shrubs of Phillyrea, probably P. angustifolia and Myrtus communis, both growing

as an understorey in the forest. The forest may have had a heavy liana population, e.g. Smilax, but this would be difficult to detect due to the high degree of under-representation of the plant. Arbutus too may have been important but as has been seen in the modern pollen survey Arbutus pollen is not exported from the forest. The soil types occupied by the Quercus forest then would be similar to those occupied by Quercus today, i.e. those with high water table levels which enable the development of monte negro hygrophytic type vegetation. The fall in Quercus that occurs at the end of the zone may be a proportional effect of the chenopod rise but may represent perturbation of the forest, a phase that is carried over into the next zone.

The other major forest forming species that was present at this time was Pinus, which, by comparison with the present vegetation, could be Pinus pinea; however, P. pinaster is also a possible candidate as is P. halepensis, a species of the more calcareous soils, types of which lie to the north of Laguna de las Madres. The type of soil occupied by Pinus is likely to be similar to that occupied by it today, i.e. dry unstable sand surfaces (evidence for unstable soils has already been seen with the high chenopod values seen).

Juniperus communities which are characteristic of dry stable soils do not appear to be present, however, Juniperus can be under-represented but it is noticeable that Juniperus peaks heavily at least twice further up the diagram, which are indicative of large populations occurring very close to the site. Pollen of Pistacia is also recorded from this zone,

which from the modern pollen survey has been shown to be under-represented and thus populations of Pistacia may have been important on the more silty soils near the site.

The shrub communities that are derived from the forest types also do not appear to be extensive in this zone. The quantities of Erica lusitanica type pollen recovered are low when compared to the modern day pollen rain. This also applies to the monte negro/blanco shrub dominated by Halimium type pollen, although the pollen rain of some of the plants of these communities in under-represented, e.g. Genista anglica and pollen of Mentha type producing plants is not exported from the systems.

Long distance pollen input is a feature of the site at this time, i.e. Alnus, Corylus, Picea. The origin of Alnus and Corylus is thought to be the deep humid gorges of the Sierra Morena, though Alnus does still extend some way down the floodplain of the Guadalquivir (G. Novo, personal communication). Picea must have come from further afield for it is not recorded from the Iberian peninsula today.

Pollen Assemblage Zone LM2-2

Local

This zone is characterised by increasing Isoetes and a peak in Nuphar, which suggests increasing water levels, which would also inundate the surrounding land and provide suitable shallow water conditions for Isoetes to colonise. The cause of the rise in water level may be correlated with the blocking

of the outflow of the Laguna into the sea by mobile sand dune activity. Telmatic peat formation begins at 208cm. and this zone is a prelude to this event.

Evidence of disturbed soils is still strong. The chenopods are high but decrease during the zone, which may indicate some stabilization of the soils, however, values of the Liguliflorae now rise to a high level, which themselves are indicative of soil disturbance as are the Cruciferae which also rise. The cause of this disturbance may be correlated with either forest perturbation, or the rise in water level.

Regional

Regionally Quercus and Pinus both decline, the cause of which may be a proportional effect of the large rise of the Liguliflorae, however, this effect appears to be taken up by the Chenopodiaceae. Since Phillyrea also declines and disappears, evidence points to a large perturbation of the forest systems which could be caused by:-

i) Anthropogenic effects - however, no direct evidence of mans' activity is recorded from this zone.

ii) Advancement of the mobile dune system, is a distinct possibility for the outflow appears to have been blocked by them.

The disturbance of the forest however, brings about no increase in pollen types typical of the shrub communities, i.e. monte negro hygrophytic.

Pollen Assemblage Zone LM2-3

Local

The local conditions in the Laguna at this time undergo a profound change, with a switch from lake deposits to telmatic peat formation at 208cm. The pollen changes associated with this switch are :-

i) decrease in *Isoetes*, *Nuphar*

ii) increases in Filicales, *Sparganium* type, Cyperaceae and *Typha latifolia* and Gramineae.

The cause of peat formation may be explained by normal hydroseral successional changes, with the Laguna becoming invaded with plants that are indicative of swamp conditions, howvever, a fall in the water levels of the Laguna may also have occurred which may be related to rainfall, such processes are known to control water levels in some East Anglian meres in Britain that have a pervious bottom. (Coombe *et al*, 1981). A further complication of the story is that the fall may have been caused by tectonic activity, for it is known that the region has been subjected to much minor tectonic movement (Chapter 5). The soils surrounding the Laguna appear to have stablized with the decrease in Liguliflorae and Chenopodiaceae curves which may indicate the cessation of dune movement and/or mans activities.

It is significant that the fall in the Chenopodiaceae values is continued into the peat formation phase of this zone, for this is further evidence that the origin of the chenopod pollen must have been disturbed ground rather than salt marsh vegetation, it also suggests that at least some of the

chenopod pollen is aerially transported rather than in eroded soils.

The site at this time was probably dominated by swamp vegetation, the build up in Gramineae values being the result of invasion of the swamp by Phragmites australis. The increase in Sparganium type and Typha latifolia could represent the colonisation of the wetter margins of the Laguna. Indications that a damp grassland may have surrounded the Laguna at this time comes from the presence of Illecebrum pollen, a type that is characteristic of wet grassland systems of the area.

Regional

This zone seens increasing Quercus and Pinus, the Quercus increase being accompanied by a peak in Erica lusitanica type which is the first indication of the development of the derived monte negro hygrophytic shrub vegetation, which suggests the recolonisation of soils from which the Quercus had previously been removed, and thus the cessation of disturbance which has been evident throughout the previous two zones. The Quercus rise is interrupted slightly in the zone but after this phase it continues its rise, which is associated with a decline in values of Erica lusitanica type, which may indicate a succession occurring to Quercus. The development of the vegetation on the drier soils appears to have been dominated by Pinus, the presence of which suggests that the dry soils surrounding the Laguna had not yet stabilized enough to allow colonisation by Juniperus as seen later in the diagram.

Due to under-representation of most of the other forest and shrub types, little information can be gained about the role they play in the vegetation, although Pistacia pollen is recorded which must indicate the presence of dry stable, silty soils nearby.

Pollen Assemblage Zone LM2-4

Local

The local pollen assemblage in this zone once again undergoes a profound change from a community dominated by Sparganium type, Typha angustifolia, T. latifolia, to one in which the Filicales and Cyperaceae become prominent, reflecting either a drop in water level due to tectonic events or is the result of a normal hydrosere raising the peat surface above the water level. The Filicales however, decline to the end of the zone after having achieved very high levels. The fern species responsible for the spore input in thought to have been a group of ferns that key out to Thelypteris palustris type, which includes some Asplenium and Phyllittis species as well (Moore and Webb 1978). Because of the evidence of the wet conditions during this time then T. palustris seems a reasonable choice for the species involved, since it occupies similar habitats in the rest of europe, however, the species does not appear to be recorded from Spain (Flora Europaea Vol.1). The species has however, been recorded in the previous study of the site by Menendez Amor and Florschutz (1964). Thus the problem of the species responsible remains unresolved.

Further evidence that this site was undergoing a reduced wetness comes from the invasion of the surface by other wet-

land plants such as Galium type, Lythrum and Hydrocotyle. The Gramineae values have declined from the previous zone and could reflect reduced Phragmites domination. Small ephemeral pools containing Myriophyllum alterniflorum and Potamogeton appear also to have been formed at this time. This phase of dryness of the diagram tends to be repeated to a lesser extent in LM1-2.

A major phase of disturbance around the edges of the Laguna appears to have occurred at the beginning of the zone as indicated by a large peak of Salix, it is not only the local Laguna environment that appears to be disturbed for the disturbance is repeated in the Pinus forest.

Regional

Quercus continues to rise in this zone, the depression at the beginning possibly being the effect of the increase in Salix. Thus Quercus appears to be colonising even more new ground, this process of colonisation is also reflected in the peak of Erica lusitanica type pollen recorded from the beginning of the zone, the fall in this type occurring as Quercus reaches its highest levels so far at the end of the zone. The Quercus maximum is also accompanied by a decrease in Phillyrea, an event that would appear if Phillyrea now became consigned to the trunk space of Quercus rather than the canopy component of the derived shrub vegetation.

A different turn of events is occurring to Pinus, for the pollen values become very erratic in this zone, accompanying this behaviour are indicators of disturbance, e.g. Cruciferae and Polygonum persicaria. It is not as if Pinus is being

replaced by a different forest type like Juniperus, however, the disturbance results in no appreciable input of the derived shrub type, i.e. monte blanco shrub. An anthropogenic cause may be postulated for the behaviour of the Pinus for if mobile sand dunes had become active once again this would reveal itself in the stratigraphy, which did not occur. The values of Pinus do recover to a peak at the end of the zone, only for the disturbance to be repeated even more severely in the next zone.

Detection of events in the other forest/shrub communities is still difficult, Pistacia now becomes a constant feature of the diagram for the first time. Of some significance also is the first appearance of Olea pollen, which may be indicative of olive cultivation in the region. As seen from the modern pollen, although the tree is highly productive the resulting pollen is poorly dispersed. Olea may also be a naturally occurring member of the mediterranean forest occupying the hotter regions of the area, possibly with Ceratonia siliqua a tree that will be seriously under-represented since it belongs to the Leguminosae.

Pollen Assemblage Zone LM2-5

Local

The local flora of the site now undergoes another change as the Filicales and Cyperaceae decrease to low levels, which is followed by a steep increase in Nymphaea, which is indicative of the formation of open water again. Before the Filicales and Cyperaceae fall strong peaks in wetland plants

occur such as:- Lythrum, Galium type, Potamogeton and a solitary peak in Typha latifolia, which all collapse as the Cyperaceae and Filicales fall.

Regional

Disturbance and changes are very evident in the regional forests in the zone. Values of Erica lusitanica type peak again which this time is indicative of disturbance of the Quercus forest which falls and recovers and then repeats the same process again before the end of the zone. The cause of the depression in the Quercus values could be:-

i) Falling water tables. This is unlikely since conditions in the Laguna became wetter during this zone, however, an expansion of Juniperus does occur in this zone which may indicate the extension of stable dry soils. The Juniperus expansion seen in this zone follows the almost complete disappearance of Pinus from the pollen record, which would be expencted if soils had stabilized sufficently for Juniperus to invade. The values of Juniperus recovered from this zone (by comparison with the modern pollen rain) suggest a sizeable population surrounding the Laguna at this point. Thus the Juniperus expansion may be correlated with the Pinus disappearance rather than expansion onto soils previously colonised by monte negro hygrophytic vegetation. However, this sequence of replacement is not followed for the second Juniperus peak higher up the diagram.

ii) The second cause of disturbance, would be of an anthropogenic form, this is the more plausible explanation for events in the Quercus forest for peaks occur in very many types indicative of human interference:- Rumex type, Plantago type, Chenopodiaceae Polygomun persicaria, Artemisia. The peaks in Rumex type and Plantago type ate the first occurrence of of such events and it is possible that some of the mediterranean Quercus forest was degraded to a pasture type condition "pastizal" (Table 3), which may have been maintained by grazing. The peak in Gramineae >40 μ also suggests human influences on the vegetation and could be indicative of agriculture. The low Phillyrea values found in this zone tend to support the hypothesis of interference with the forest types until "pastizal" conditions were formed on removal of monte negro hygrophytic shrub community.

Pollen Assemblage Zone LM2-6

Local

Open water conditions are maintained during this zone with large amounts of Nymphaea pollen recorded, consequently values of the wetland plants are low during this zone. A major disturbance of the Laguna edges occurs as indicated by the sustained peak of Salix found in this zone, which may be correlated with a mineral inwash found between 90-100cm.

Regional

Quercus now recovers from the disturbances of the previous zone and reaches its highest levels ever recorded from the core, after the peak the values fall away again as peaks occur once more in human indicator types:- Rumex type, Plantago, Chenopodiaceae and Erica lusitanica type. The Erica lusitanica peak is not sustained as long as the rest and indicates the return of pastizal conditions once more. Gramineae grains >40 μ and some >50 μ are recorded, which is indicative of cereal cultivation, and the high peak in Chenopod pollen probably derives from weed populations growing in these cultivated grounds. Although Quercus declines during the zone, Phillyrea, a plant normally associated with Quercus increases steadily, possibly indicating a shift from the trunk space component of Quercus into a canopy component of the derived shrub.

The Juniperus population seen in the previous zone has now fallen, a possible cause of the disappearance could be destabilization of the soils (which undoubtedly is occurring, since Salix peaks but Juniperus occupies drier soils and Salix the wetter and are unlikely to be correlated). The fall in Juniperus is not followed by a massive expansion of Pinus, a likely corollary if the dry soils had destablized. A rise in water tables due to tectonic activity may result in the disappearance of Juniperus and this may explain the initial Quercus increase and Salix peaks in the zone but indications of human interference in the forests is very strong especially at the end of the zone. The zone is also characterised by an increased input of Alnus and Corylus compared to previous zones.

Pollen Assemblage Zone LM2-7

Local

The local aquatic community undergoes further changes in this zone, a fall in Nymphaea and subsequent increases in Filicales and Cyperaceae suggest either a hydroseral succession raising the peat surface above the water, or a general fall in water levels, which would depend on the permeability of the Laguna bottom. The sequence of vegetation changes appears to be:-

i) Nymphaea falls, Potamogeton peaks, Cyperaceae peak

ii) " Potamogeton fall, Cyperaceae fall Myriophyllum alterniflorum peak, Filicales rise

iv) Nymphaea falls, Potamogeton fall, Cyperaceae rise M. alterniflorum fall, Filicales rise

Also a number of wetland plants reinvade the Laguna at the end of the zone, e.g. Galium type and Lythrum. Thus once again the Laguna has conditions that resemble those seen in Lm2-4. General disturbance around the edge of the Laguna appears to diminish as the Salix peak falls away.

Regional

Quercus recovers at the beginning of the zone from the disturbances of the previous zone. However, the recovery is short-lived for Quercus now undergoes continued decline. There are two possible causes of the decline:-

i) Human interference

ii)Falling water tables due to tectonic uplift.

Evidence for human interference is strong: Erica lusitanica type peaks as Quercus declines, but then falls itself. At the end of the zone there are peaks in Plantago type, Rumex type, Cruciferae and Chenopodiaceae, which may indicate extensive development of pastizal type communities. The fall in E. Lusitanica type shows the removal of shrub vegetation and its replacement by pastizal communities. Phillyrea also peaks when Quercus declines, again reflecting a move from trunk space to canopy component of the derived shrub, it then falls away as the values of E. lusitanica type fall reinforcing the hypothesis of removal of the shrub vegetation.

Evidence for falling water tables being the cause of the forest changes may also be found, the Laguna at this time does show drying out, though this may be due to hydroseral succession. However, an expansion of Juniperus also occurs which may be explained by falling water tables, the increase in Pinus may have been caused by sand dunes that had been once stable, suffering a drop in water table, which would enable them to become active again and thus Pinus would be colonising these destablized sands. However, the values of Pinus suggest an extensive population surrounding the Laguna which does not fit in with the extension of Juniperus also seen around the Laguna, and mineral inwashes may have been expected into the Laguna as a result of any sand movement caused by destabliza-tion.

The Pinus increase which despite a fall later on in the diagram, probably represents the origin of the Pinus forests now left around the Laguna, which are thought to have a human

origin, since Pinus pinea was known to be planted for wood production and for the cones which contain edible seeds. If this is so then this may explain the occurrence of pastizal indicators for the Pinus plantation today are open systems that do not have shrub dominated understoreys but a grassland dominated by Rumex and Plantago spp. Thus we be seeing here removal of the Quercus forest and subsequent derived shrub layers for Pinus cultivation, the expansion of Juniperus may have been partially facilitated by falling water tables that made conditions suitable for Pinus cultivation, with it invading Quercus forest not utilised for this purpose. The other reason for invoking a human origin for the Pinus forests is the atypical behaviour of Pinus in the light of knowledge about its present day ecology. (G. Novo 1979, Harrant and Jarry 1967).

A species not native to the Iberian peninsula appears at the end of this zone:- Juglans, a tree of the Eastern Mediterranean and thought to have been introduced by the Romans.

Continuous pollen inputs of Fraxinus are also found in this zone when compared to previous zones and may represent such a forest type.

Pollen Assemblage Zone LM2-8

Local

The local aquatic/wetland vegetation seen in the previous zone continues into this zone, but conditions appear to get slightly wetter as small increases occur in Nymphaea and

Myriophyllum alterniflorum and consequential falls in Filicales (after a recovery from the previous zone) and Cyperaceae. The present day surface was dominated by Phragmites australis and no open water was observed, due to extensive drainage of the system for peat exploitation. The possibility that the peat surface does not represent the present day surface will be further discussed in the section on core correlation of this chapter.

Regional

Quercus appears to be little affected during this zone, maintaining itself at the level seen at the end of the previous zone, however, the same cannot be said of Juniperus or Pinus. Juniperus collapses once more but still maintains a low input, which is suggestive of a sparser population of Juniperus occurring. Pinus also exhibits a fall due probably to logging of the tree. Rising water levls could explain the fall in Juniperus and Pinus but there is no response from the monte negro hygrophytic type plants, e.g. Quercus or Erica lusitanica type. The fall in Juniperus may have been caused by destablization of the soils but no corresponding increase in Pinus is observed. It is known (G. Novo, personal communication) that large areas of Juniperus were removed and this is the likely cause of the Juniperus fall.

The monte negro hygrophytic shrub vegetation which fell at the end of the last zone remains low. Pastizal conditions, probably under Pinus, are maintained (Cf.Rumex and Plantago) Phillyrea once again shows a heavy pollen input and must reflect the presence of the tree in the monte negro hygro-

phytic shrub canopy.

Pollen input from the Pistacia community becomes very irregular although Rhamnus pollen occurs, a plant which tends to be associated with Pistacia, but is a type that is under-represented. Pollen input of another non-native species occurs in this zone, i.e. Eucalyptus, a tree that was introduced in the eighteenth century as an ornamental plant but now is planted extensively, for it is fast growing, even more so than Pinus pinea. Olea input rises for the first time above the odd record and indicates the presence of olive cultivation in the region.

Laguna de las Madres 1:- Interpretation

The diagrams for this core are shown in Figs.57-63 and the stratigraphy and basis of zonation in Tables 16 and 17 respectively.

Pollen Assemblage Zone LM1-1

Local

This pollen assemblage zone includes a hiatus between 200 and 244cm where the pollen density and preservation were poor. The local vegetation undergoes a distinct change from one side of the hiatus to the other, with peat deposition beginning at 194cm, the rest of the sediment being silts and clays.

Below the hiatus occurs a community dominated by Isoetes with plants characteristic of more eutrophic systems absent. There is a characteristically high peak of Chenopodiaceae before the hiatus (Cf.LM2-1 - LM2-3) associated with Isoetes and thus it seems that soil disturbance was just not a local feature restricted to LM2 but was a general widespread event. (heavy inwash of sediments). The disturbance was probably related to activities of the mobile sand dunes which had become mobile during this time and subsequently blocked the Laguna outflow. Normal hydroseral succession took place and telmatic peat formation was initiated at 194cm.

Across the hiatus, the local pollen assemblage changes, from Isoetes domination to Cyperaceae, Myriophyllum alterniflorum

TABLE 16

Laguna de las Madres 1:- Stratigraphy

Depth cm.	Description
0-20	Peat not sampled
20-50	Humified *Phragmites* peat
50-90	Black humified peat
90-102	Brown " "
102-110	Black " "
110-135	Brown " " - *Phragmites* found
135-140	Dark brown humified peat
140-148	Brown humified peat
148-150	Black " "
150-158	Brown " "
158-164	Darn brown peat with black bands
164-166	Unhumified peat
166-169	Black band of peat
169-170	Mineral inwash
170-176	Dark brown peat - banded
176-180	Brown peat
180-182	Brown peat - silty
182-194	Black banded organic silt
194-200	Blue clay
200-260	Grey clay/sand - with black bands

TABLE 17

LAGUNA DE LAS MADRES 1

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
LM1-6	*Quercus*-*Halimium*-	*Quercus* falls, *Pinus* and *Juniperus* fall, *Erica* and *Halimium* peak, *Rumex* peak
LM1-5	*Quercus*-*Pinus*	*Juniperus* falls, *Pinus* falls
LM1-4	*Quercus*-*Salix*-*Juniperus*-*Pinus*	*Quercus* peak, *Salix* peak, *Juniperus* fall and peak, *Pinus* peak
LM1-3	*Quercus*-*Juniperus*-Chenopod	*Quercus* increase, *Juniperus* peak, Chenopodiaceae peak, Gramineae decrease. *Erica* decrease
LM1-2	*Erica*-*Phillyrea*-*Pinus*	*Pinus* erratic, *Quercus* low, *Erica* peak, Gramineae decrease
LM1-1	*Pinus*-Chenopodiaceae	*Pinus* peak, Chenopodiaceae peak, Gramineae increase, *Myriophyllum alterniflorum* peak.

Fig.57

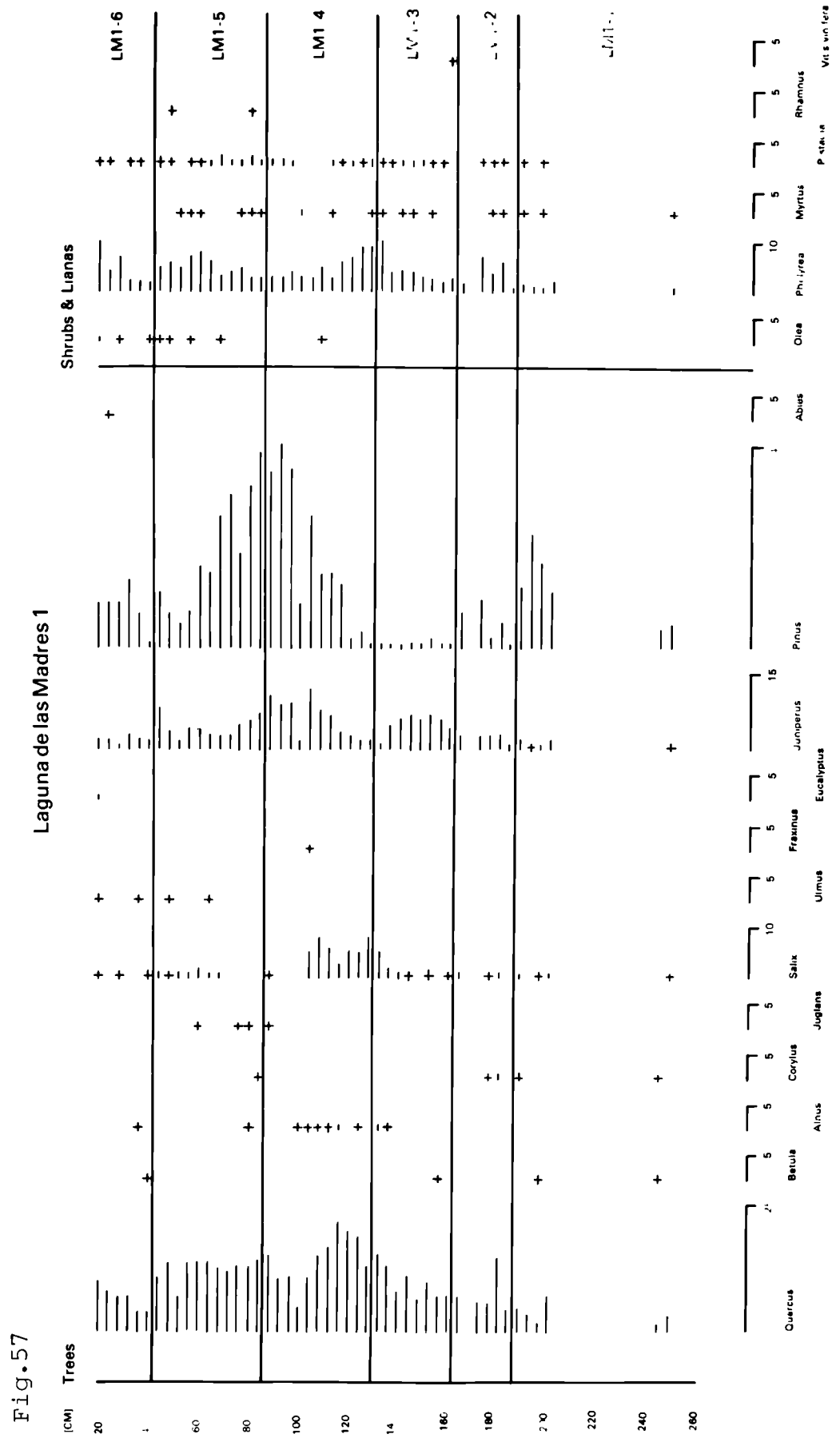

Laguna de las Madres 1
Trees
Shrubs & Lianas
(CM)
LM1-6
LM1-5
LM1 4
LM1-3
LM1-2
Quercus
Betula
Alnus
Corylus
Juglans
Salix
Ulmus
Fraxinus
Eucalyptus
Juniperus
Pinus
Abies
Olea
Myrtus
Rhamnus

Fig.58

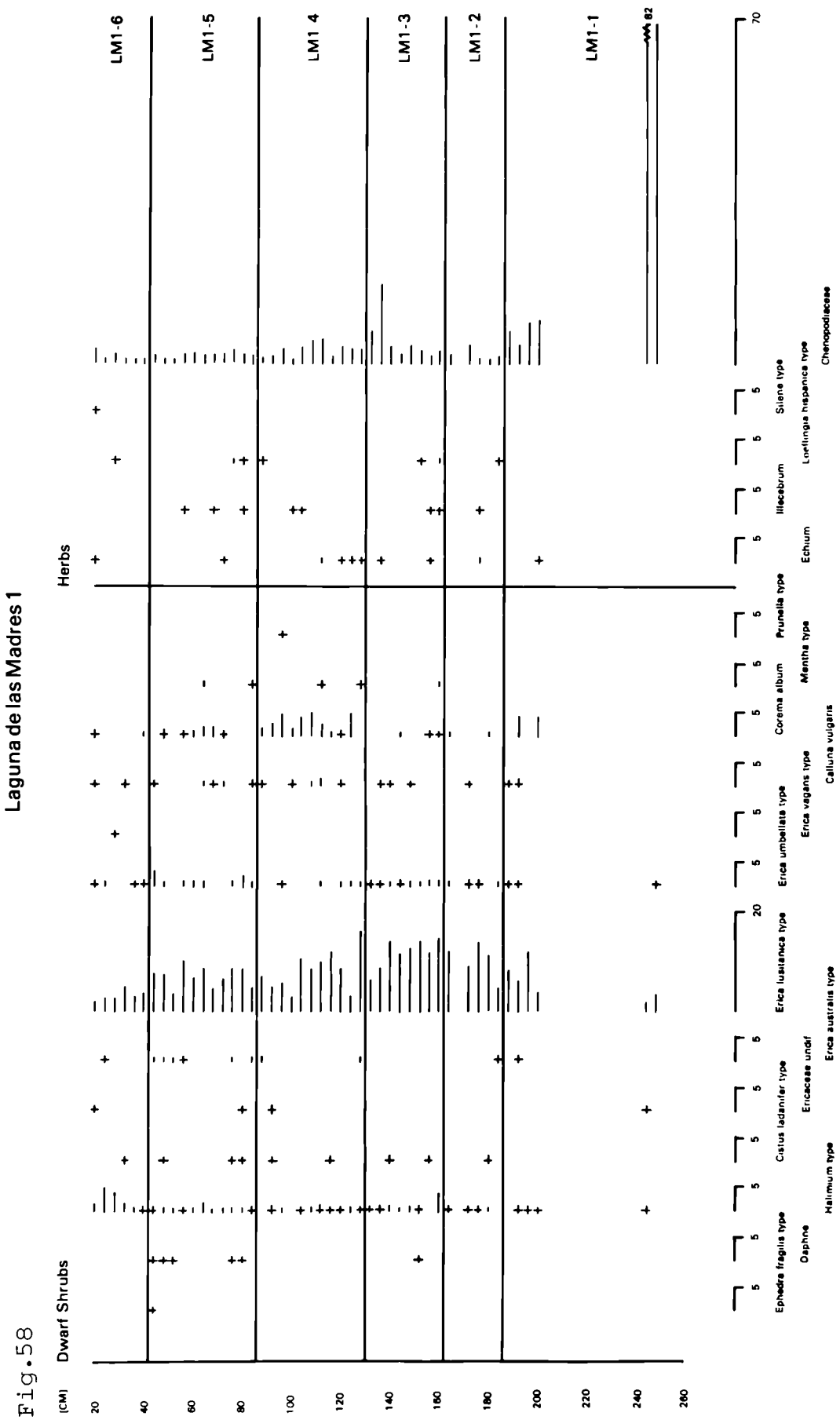

Laguna de las Madres 1
(CM)
Dwarf Shrubs
Herbs
LM1-6
LM1-5
LM1 4
LM1-3
LM1-2
LM1-1
82
20
40
60
80
100
120
140
160
180
200
220
240
260
Ephedra fragilis type
Daphne
Halimium type
Cistus ladanifer type
Ericaceae undif
Erica australis type
Erica lusitanica type
Erica umbellata type
Erica vagans type
Calluna vulgaris
Corema album
Mentha type
Prunella type
Echium
Illecebrum
Loeflingia hispanica type
Silene type
Chenopodiaceae
70

Fig.59

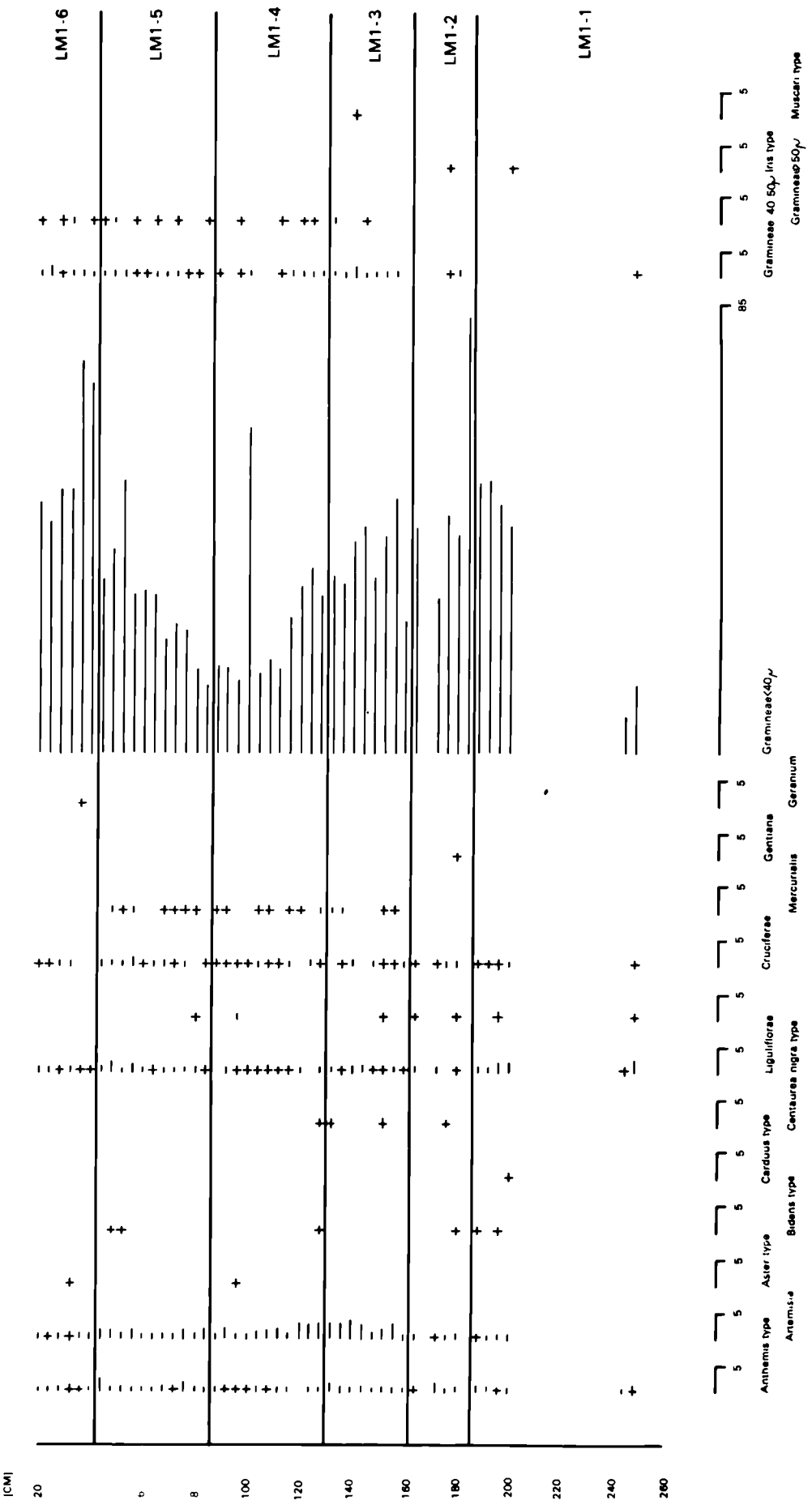

Laguna de las Madres 1
LM1-6
LM1-5
LM1-4
LM1-3
LM1-2
LM1-1
[CM]
20
60
80
100
120
140
160
180
200
220
240
260
Anthemis type
Aster type
Bidens type
Carduus type
Centaurea nigra type
Liguliflorae
Cruciferae
Mercurialis
Gentiana
Geranium
Graminease<40μ
Graminease 40 50μ Iris type
Graminease 50μ Muscari type
Serratula type

Fig.60

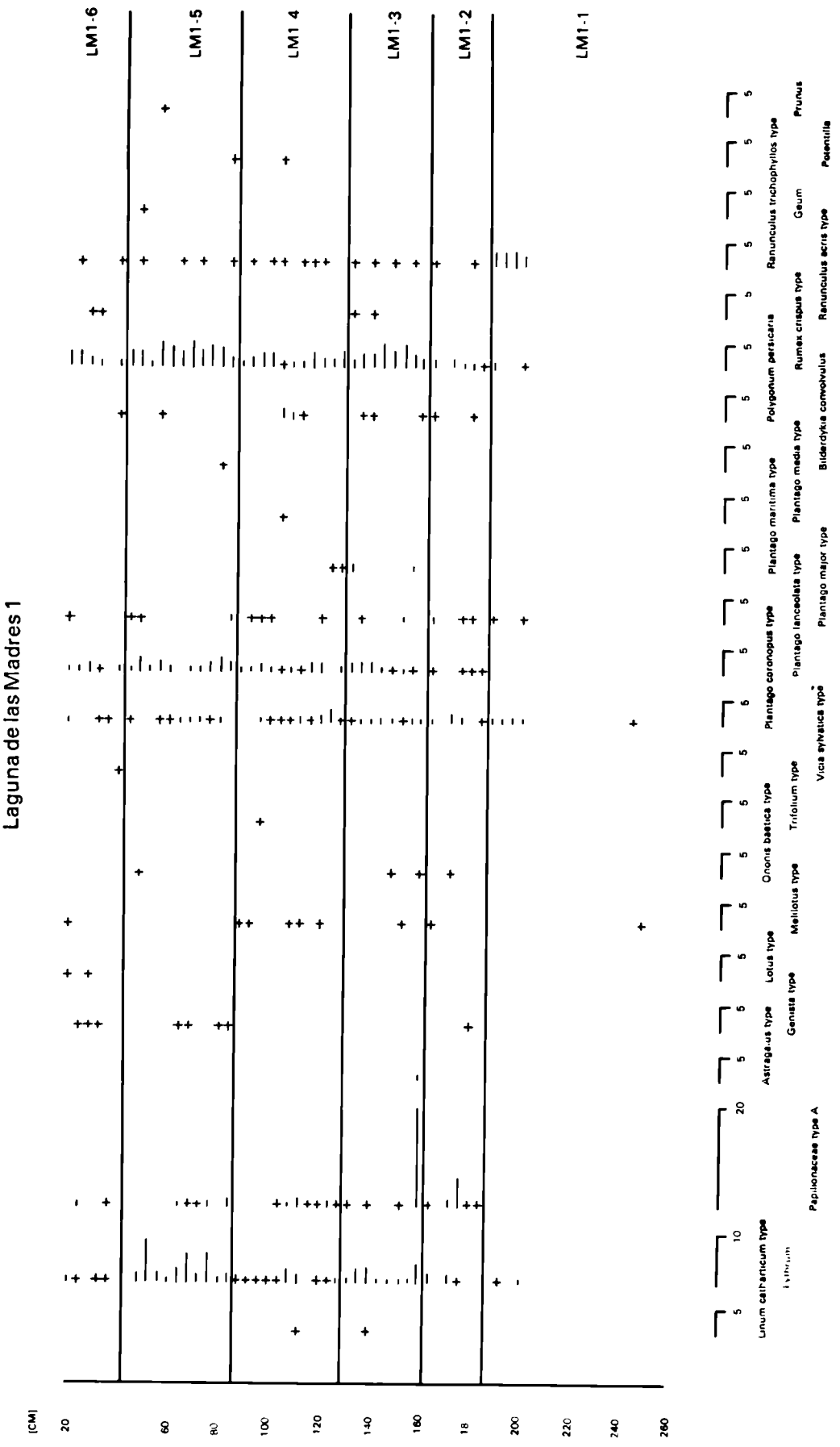
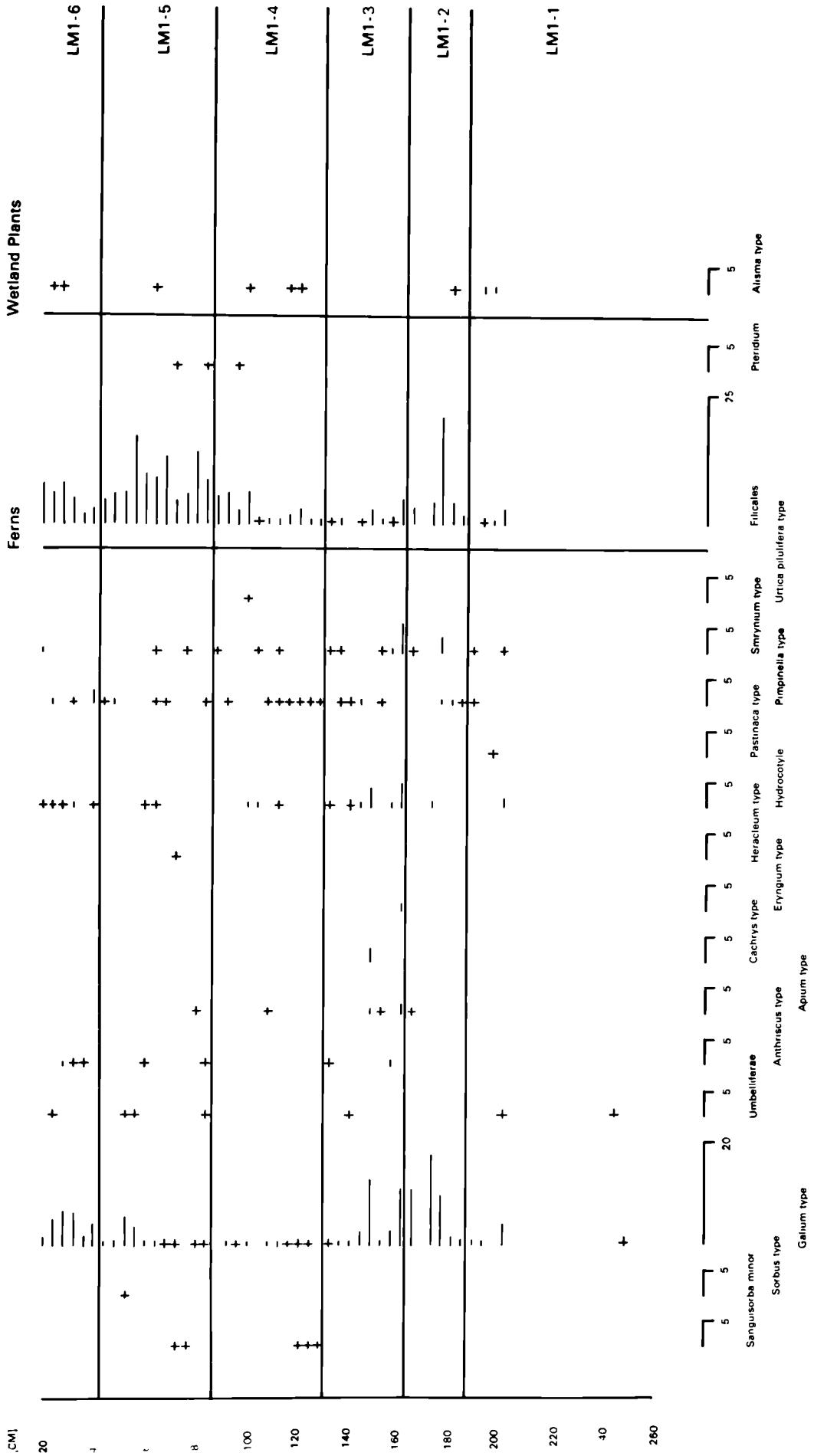

Laguna de las Madres 1
[CM]
LM1-6
LM1-5
LM1 4
LM1-3
LM1-2
LM1-1
Linum catharticum type
Papilionaceae type A
Astragalus type
Lotus type
Genista type
Melilotus type
Ononis bastica type
Trifolium type
Vicia sylvatica type
Plantago coronopus type
Plantago lanceolata type
Plantago major type
Plantago maritima type
Plantago media type
Bilderdykia convolvulus
Polygonum persicaria
Rumex crispus type
Ranunculus acris type
Ranunculus trichophyllos type
Geum
Potentilla
Prunus

Fig.61


Laguna de las Madres 1
Ferns
Wetland Plants
LM1-6
LM1-5
LM1-4
LM1-3
LM1-2
LM1-1
Sanguisorba minor
Sorbus type
Galium type
Umbelliferae
Anthriscus type
Apium type
Cachrys type
Eryngium type
Heracleum type
Hydrocotyle
Pastinaca type
Pimpinella type
Smyrnium type
Urtica pilulifera type
Filicales
Pteridium
Alisma type

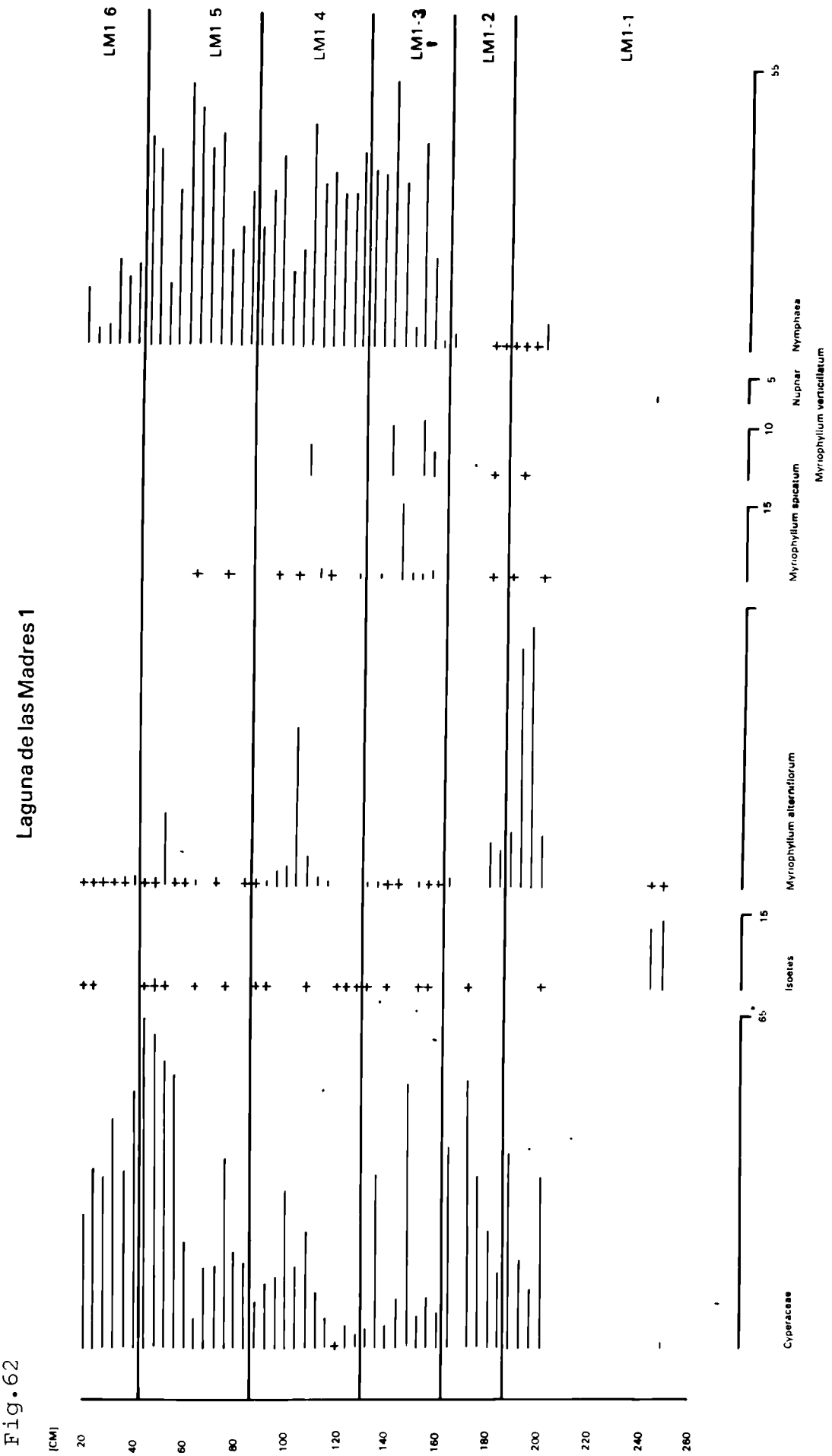

Laguna de las Madres 1
LM1 6
LM1 5
LM1 4
LM1-3
LM1-2
LM1-1
(CM)
20
40
60
80
100
120
140
160
180
200
220
240
260
Cyperaceae
65
Isoetes
15
Myriophyllum alterniflorum
15
Myriophyllum spicatum
10
Nuphar
5
Nymphaea
Myriophyllum verticillatum
55

Fig.62

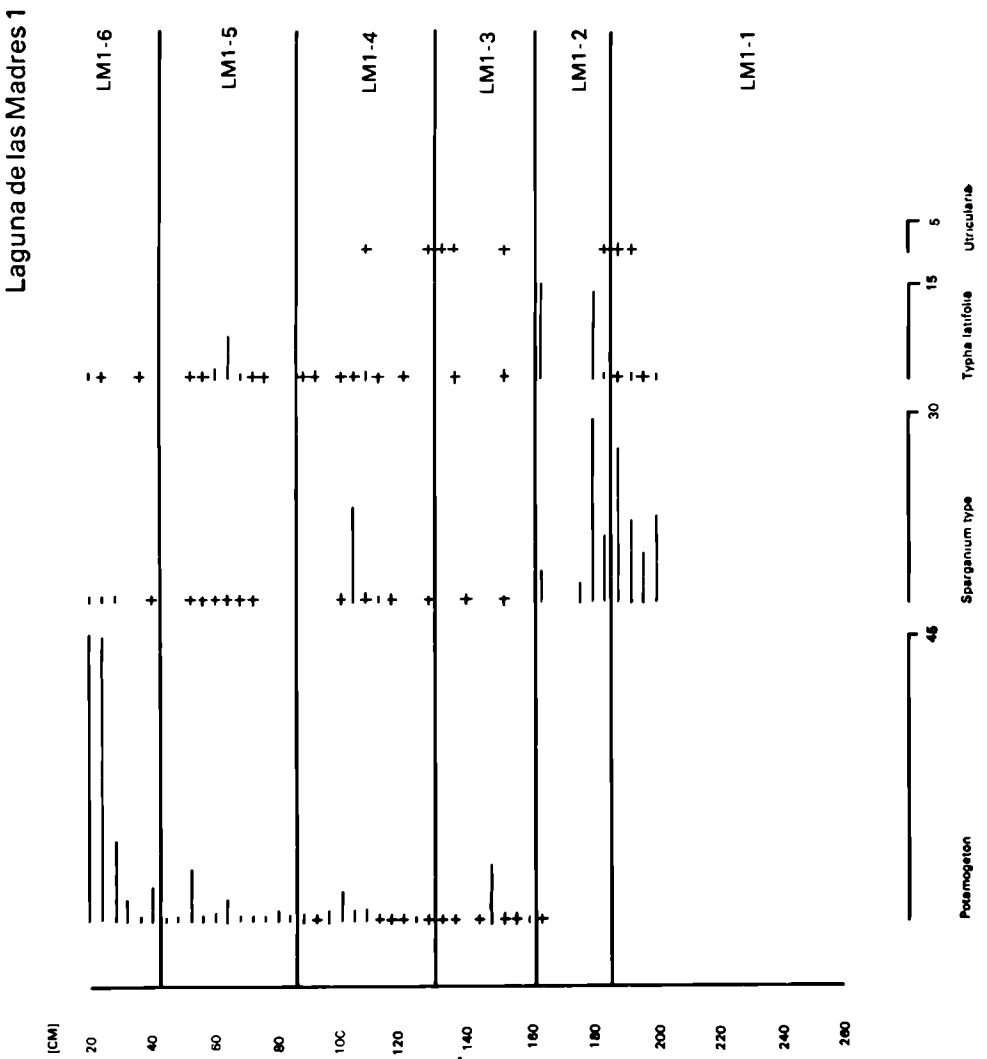

Laguna de las Madres 1
LM1-6
LM1-5
LM1-4
LM1-3
LM1-2
LM1-1
[CM]
20
40
60
80
100
120
140
160
180
200
220
240
260
45
30
15
5
Potamogeton
Sparganium type
Typha latifolia
Utricularia

Fig.63

and Sparganium type, and Ranunculus trichophyllus type which is suggestive of swamp conditions with some open water, though not enough for Nymphaea to occur, Gramineae also increase steeply on this side of the hiatus probably reflecting the invasion of the site by Phragmites australis. This first stage of hydroseral succession is very similar to that of LM2-3 although indications of wetter conditions occur here.

Regional

Quercus and Pinus are very low at the beginning of the zone, however, above the hiatus, Quercus peaks, declines and recovers, Pinus only peaks and declines. The depression in Quercus is correlated with the first appearance of the derived shrub communities of the Quercus forest. Soil conditions are still unstable during this zone as indicated by the peak in Corema, Pinus and Chenopodiaceae. This instability may explain the low occurrence of Phillyrea, a shrub that will grow in the monte negro hygrophytic shrub communities if conditions are stable enough (G. Novo 1977), and the low values of Juniperus and Quercus found in this zone, both of which require stable conditions.

Pollen Assemblage Zone LM1-2

Local

The local swamp vegetation indicates that a drier community developed compared with the previous zone, since Myriophyllum alterniflorum, a plant of open water disappears and the invasion of Galium type, Typha latifolia and Filicales, which all require slightly drier conditions. The reduced amount of

Gramineae found in this zone, reflecting the decreased importance of Phragmites as the peat surface is raised to produce drier conditions.

Regional

The forest/shrub types fluctuate markedly during this zone. Quercus increases gradually except for one abnormally large peak. The increase is also accompanied by increases in monte negro hygrophytic shrub as indicated by Erica lusitanica type and may correlate with expansion onto stablized wetter soils around the Laguna. Thus the forest appears to be recovering from its previously disturbed phase. Evidence of more stable conditions comes from the low amounts of Chenopods present and the peak of Phillyrea, a plant that requires stable conditions which may have been provided in the shrub community rather than the forest community.

The dominance of Pinus and Quercus pollen resembles that of the present time. Pinus meanwhile becomes very erratic, a situation that is very similar to that recorded from LM2-4, and is associated with the appearance of Juniperus in quantities that by reference to modern day pollen studies may indicate a large population. This phase of Juniperus expansion is carried even further in the next zone. This phase in Pinus and Juniperus is analogous to the processes seen in LM2-4 and LM2-5. The cause of the change may reflect increasing stablization of soils, with Juniperus now being able to replace Pinus.

Pollen Assemblage Zone LM1-3

Local

A complex set of events now takes place in the local pollen assemblage, generally the zone shows evidence of flooding and invasion by Nymphaea, but the process is interrupted and leads to temporary re-establishment of the drier conditions of the previous zone. The sequence of events is as follows:-

i) Low Nymphaea, Low Cyperaceae. Hydrocotyle and Galium type peak - Dry phase

ii) High Nymphaea, Low Cyperaceae, Myriophyllum verticillatum peak - Flooding phase

iii) Low Nymphaea, High Cyperaceae, Hydrocotyle and Galium peak, High Potamogeton - Drier phase

iv) High Nymphaea, high Myriophyllum spicatum, high M. verticillatum - Flooding phase

This flooding phase seems to have been a general event of the Lagunas for the same characteristics were found in LM2-5.

Regional

Quercus during this zone increases steadily, so the forest still continues to be relieved of disturbance for the time being, reaching its maximum extent in the next zone. Associated with the increase in Quercus is a decline in Erica lusitanica type, which suggests successional processes removing the shrub and its replacement by forest. Two small depressions occur in the Quercus curve are correlated with

temporary peaks in E. lusitanica type, which may reflect some disturbance of the forest, however, the major disturbance indicators do not rise until the end of the zone, only Rumex type is high during this phase of Quercus increase. The increase in Phillyrea seen at the end of the zone cannot be explained as a result of transfer of the shrub from an understorey in the Quercus forest to the canopy component of the shrub community. However, since Quercus does not reach its peak until the next zone, it may be that the Quercus forest has not closed and thus pollen flow may still be free as in the more open monte negro/blanco communities. Thus we are seeing the completion of successional changes leading to the development of full Quercus forest.

The forests of the dry soils is now dominated by Juniperus, the values of which suggest a sizeable population occurring around the Laguna, the expansion of the Juniperus may well be due to stablization of the drier soils for Pinus is now almost absent from this zone. This replacement process does not occur further up the diagram with the second Juniperus peak. The Pistacia input becomes very constant in this zone and may be an indication of it being co-dominant with Juniperus on the dry soils.

General disturbance is present throughout the zone as indicated by the continued peak in Rumex type and Artemisia, however, Plantago is not seen to peak in the early stages of the zone with these two genera. However, at the end of the zone evidence of a large disturbance occurs:- Juniperus declines heavily, Plantago peaks, Chenopodiaceae peak, Salix peaks and Gramineae >50 μ. Thus a massive perturbation of

Juniperus appears to have occurred, there are three possible causes of the disturbance:.

i) An anthropogenic effect, for which evidence is great since a large number of such indicators peak

ii) Rising water tables, which would lead to an increase in Quercus, but although there has been a tendency for the Laguna to become wetter during this phase, the first occurrence of this was when Juniperus was first expanding and Quercus also had been expanding during this period of expansion.

iii) Destablization of soils would lead to Juniperus decline, however, no increase is recorded from Pinus and the water table is higher rather than falling.

Of additional interest is the recovery of Vitis from the beginning of the zone, the implications of which will be discussed later on in this chapter.

Pollen Assemblage Zone LM1-4.

Local

Minor changes occur to the local pollen assemblage in this zone, as Nymphaea decreases and is replaced by peaks of Cyperaceae, Myriophyllum alterniflorum, Potamogeton and Sparganium type which all indicate lower water levels. However, Nymphaea increases once more only to fall towards the end of the zone and be replaced by a small increase in Filicales. The Gramineae have a massive peak at 100cm which proportionally reduces all the other taxa.

Regional

Salix falls in the middle of the zone, indicating that the disturbance of the Laguna seen at the end of the last zone is now finished. Quercus rises to its maximum extent in this zone but then falls heavily as seen in LM2-6/7; this fall is associated with a general fall in Phillyrea values after having reached a massive peak in the last zone, the initial steep fall may reflect the confinement of Phillyrea to the trunk space component of Quercus forest rather than the canopy component of the derived shrub. However, when Quercus undergoes further disturbance Phillyrea does not respond.

The fall in Quercus recorded from this zone is exactly analogous to that in LM2-6/7. Two possible causes of the decline can be postulated:-

i) Anthropogenic disturbance

ii) Falling water tables due to small amounts of tectonic uplift.

A fall in water levels is a possibility for here Juniperus is seen to expand to its highest figures recorded yet and the increase in Pinus may be explained as the drier soils become even drier and destablize thus providing suitable habitats into which Pinus can invade. However, the values of Pinus recorded suggest a large population growing around the Laguna which if growing on destabilized soils would be expected to show up in the stratigraphy of the site as mineral inwash. No such evidence occurs, yet a large population must have existed around the Laguna. Thus the

possibility of an anthropogenic cause for the Pinus rise may be sought. Evidence for human interference in the vegetation is very strong in this zone with pastizal type indicators like Plantago and Rumex type peaking very strongly. It is known that the present day Pinus forests surrounding the Laguna have a grassland understorey rather than a shrub understorey. Thus the large peaks of Plantago and Rumex can derive from such a situation. A possible scenario for the forest changes that are seen to occur in this zone may be that the Quercus forest declines possibly due to falling water tables but more likely due to actual human interference, then Pinus is planted in the place of Quercus, whose understorey is kept free of shrubs. However, these processes do not explain the massive rise in Juniperus and falling water tables may be the cause of this increase after all. A significant constant input of long distance pollen occurs in this zone as indicated by Alnus, Juglans also is recorded from this zone.

Pollen Assemblage Zone LM1-5

Local

Fluctuating water levels are indicated in this zone as Nymphaea declines and is replaced by Filicales, Galium type, Lythrum and Typha latifolia before Nymphaea once again expands at the end of the zone, surprisingly accompanied by the Cyperaceae for the two taxa have had a general inverse relationship up until now, e.g. LM2.

Regional

Marked changes are again happening in some of the forest

types, Quercus has recovered slightly from the collapse of the previous zone, but does not reach the high levels seen at the beginning of LM1-4. Disturbance of the Quercus forest may be occurring at the end of the zone (the low at 52cm is due to an abnormal Gramineae peak). However, the Quercus dominated community appears to be a relatively stable entity during this zone, as the Quercus values maintain themselves at a constant level. The other forest types undergo more drastic alterations; both Juniperus and Pinus values fall, indicating the removal of large areas of forest. While a rise in water levels could explain the Juniperus decline, the monte negro hygrophytic forest/ shrub communities do not respond as would be expected, it is probable that an anthropogenic explanation for the decline in both sets of values can be invoked, especially since pastizal indicators e.g. Rumex type are very high during this zone and thus the trees are being probably logged for wood production, which may explain the peak in Salix, if the logging had caused disturbance of the Laguna edges.

For the first time, clear indications of a Pistacia dominated community occur with a minor peak in Pistacia pollen. Olea also makes its first sustained appearance in this zone and is probably indicative of olive cultivation.

Pollen Assemblage Zone LM1-6

Local

Locally Nymphaea is replaced by a Potamogeton dominated

community, possibly drier than was seen at the end of the last zone, since peaks also occur in common wetland plants like Galium type and Filicales.

Regional

Quercus rises after an initial fall, whilst Pinus also behaves similarly but falls again after peaking and Juniperus falls away to low levels. High levels of Gramineae pollen possibly caused by invasion of the swamp by Phragmites australis may have depressed the first two values of many taxa at the beginning of the zone. Obviously the Juniperus removal seen in the previous zone is sustained here, the population not being allowed to recover as seen previously. The fluctuating Pinus values may also indicate some additional management of the Pinus plantations. The monte negro hygrophytic shrub vegetation dominated by Erica lusitanica type pollen, also decreases during this zone as the values for that pollen type fall away. This appears to be correlated with the spread of monte blanco/negro shrub communities, for values of Halimium type peak for the first time in the diagrams examined so far. However, the peak in Halimium may also have been caused by the incidence of fire, for it is known that Halimium halimifolium responds very well to fire, and similar processes were thought to have taken place in the Asperillo sand dune systems.

Laguna de las Madres 3 -: Interpretation

The pollen diagrams are given in Figs. 64-68 and the stratigraphy and basis for zonation in Tables 18 and 19 respectively.

Pollen Assemblage Zone LM3-1

Local

The local pollen assemblage of this zone suggests wet conditions of a wet meadow type of environment with Cyperaceae and Filicales. There is no evidence of extensive flooding and compared with the previous cores no indication of an *Isoetes* / Chenopodiaceae / Liguliflorae peak.

Regional

The most striking characteristic about this zone is the high input of *Vitis* pollen, the amounts of which are very large in comparison with modern day pollen rain studies of natural *Vitis* populations (Cf Dl13). Thus although *Vitis* is a natural member of the Mediterranean forest the quantities recorded here, indicate an input from a very large *Vitis* population which must have been cultivated at this time.

The Mediterranean forest types during this period behave differently, for *Quercus* values are very low throughout this zone and probably indicates the scarcity of *Quercus* forest at this time, while *Pinus* however is common at the beginning of the zone but gradually disappears during it. *Juniperus* does not replace *Pinus* as would be expected if natural succession were occurring, the suggestion is that

TABLE 19

LAGUNA DE LAS MADRES 3

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
LM3-3	Gramineae-Cyperaceae	Gramineae increases, *Quercus*, *Pinus*, *Phillyrea*, *Halimium* all low.
LM3-2	Gramineae-*Phillyrea*	*Quercus* peaks, *Pinus* falls, *Vitis* absent, *Erica* falls, *Halimium* falls, Gramineae increase.
LM3-1	*Pinus*-*Vitis*-*Halimium*	*Quercus* low, *Pinus* falls, *Myrtus* peaks, *Vitis* high, *Halimium* high, Gramineae decreases.

TABLE 18

Laguna de las Madres 3 -: Stratigraphy

Depth cm	Description
0-84	Not sampled
84-91	Highly disturbed peat
91-188	Uniform *Phragmites* peat
188-196	Scattered wood fragments
196-207	*Phragmites* peat
207-211	Red wood
211-223	*Phragmites* peat
223-224	Red wood
224-228	*Phragmites* peat
228-235	Scattered wood fragments
235-246	*Phragmites* peat
246-248	Pale wood fragments
248-253	*Phragmites* peat
253-255	Silt band
255-267	Fine detritus mud
267-268	Silt band
268-277	Fine detritus mud
277-282	Silt
282-287	Coarse organic sand

Fig.64

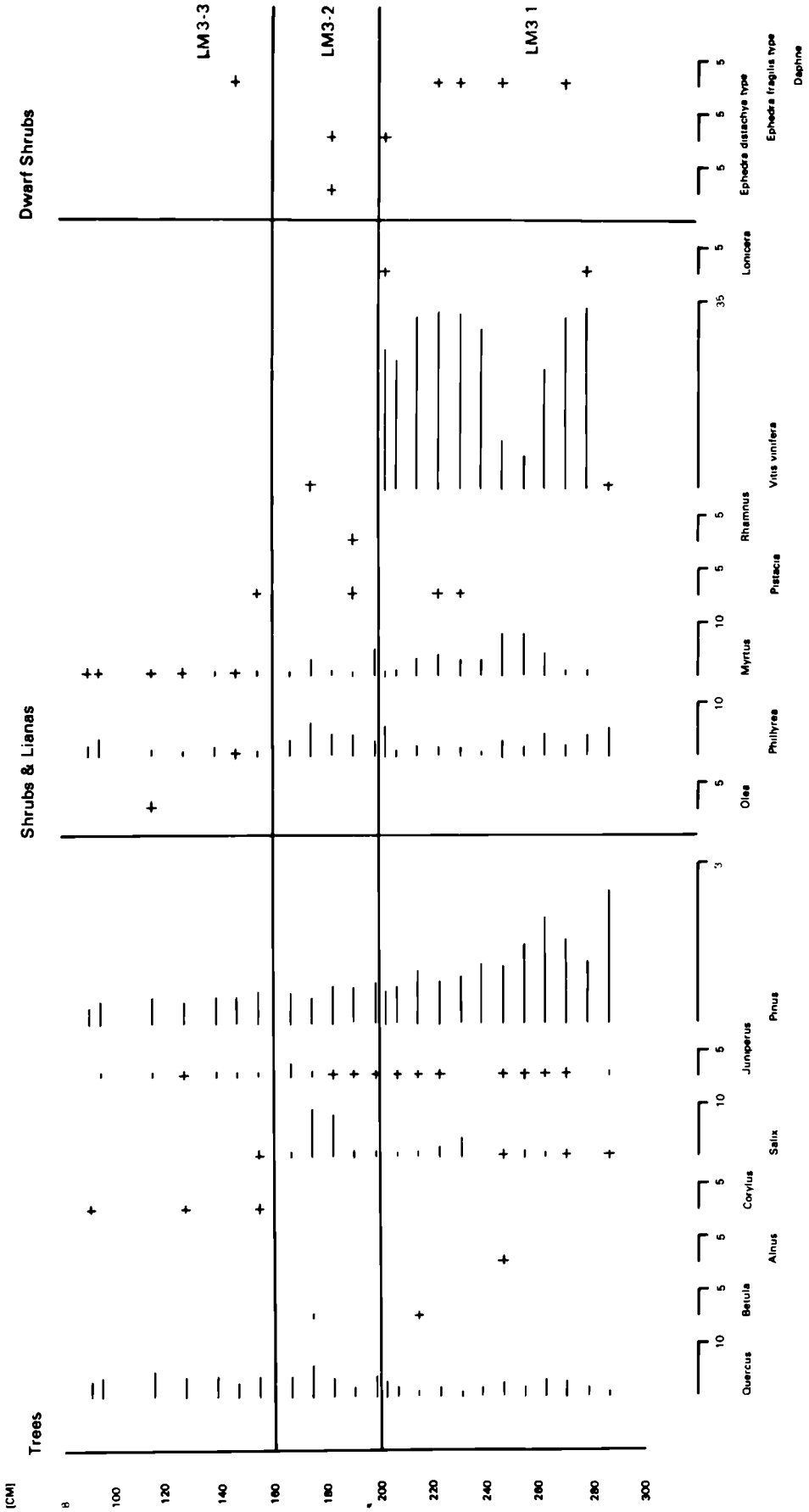

Laguna de las Madres 3
Trees
Shrubs & Lianas
Dwarf Shrubs
[CM]
LM3-3
LM3-2
LM3 1
Quercus
Betula
Alnus
Salix
Corylus
Juniperus
Pinus
Olea
Phillyrea
Myrtus
Pistacia
Rhamnus
Vitis vinifera
Lonicera
Ephedra distachya type
Ephedra fragilis type
Daphne

Fig.65

Laguna de las Madres 3

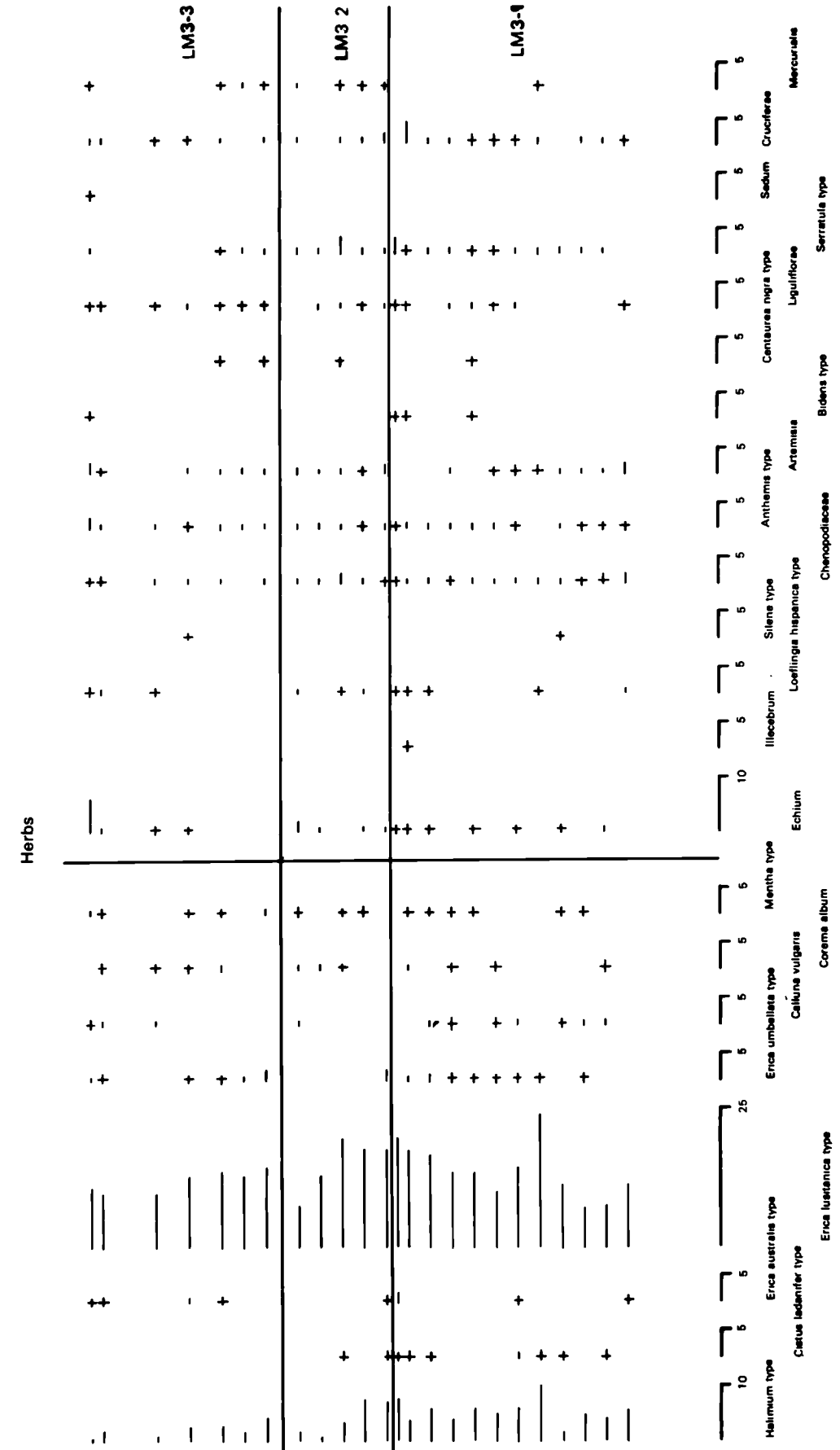


Fig.66

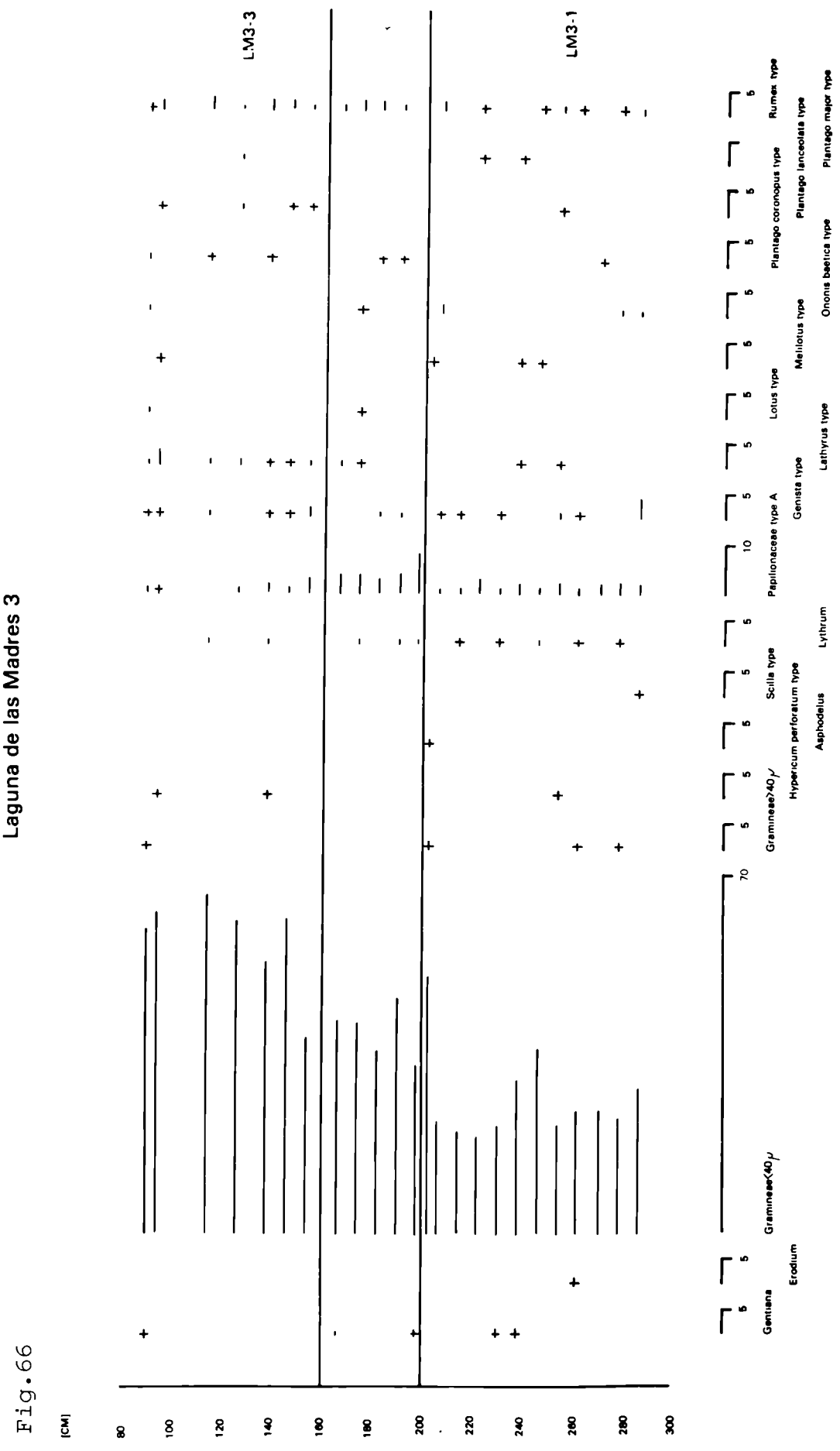
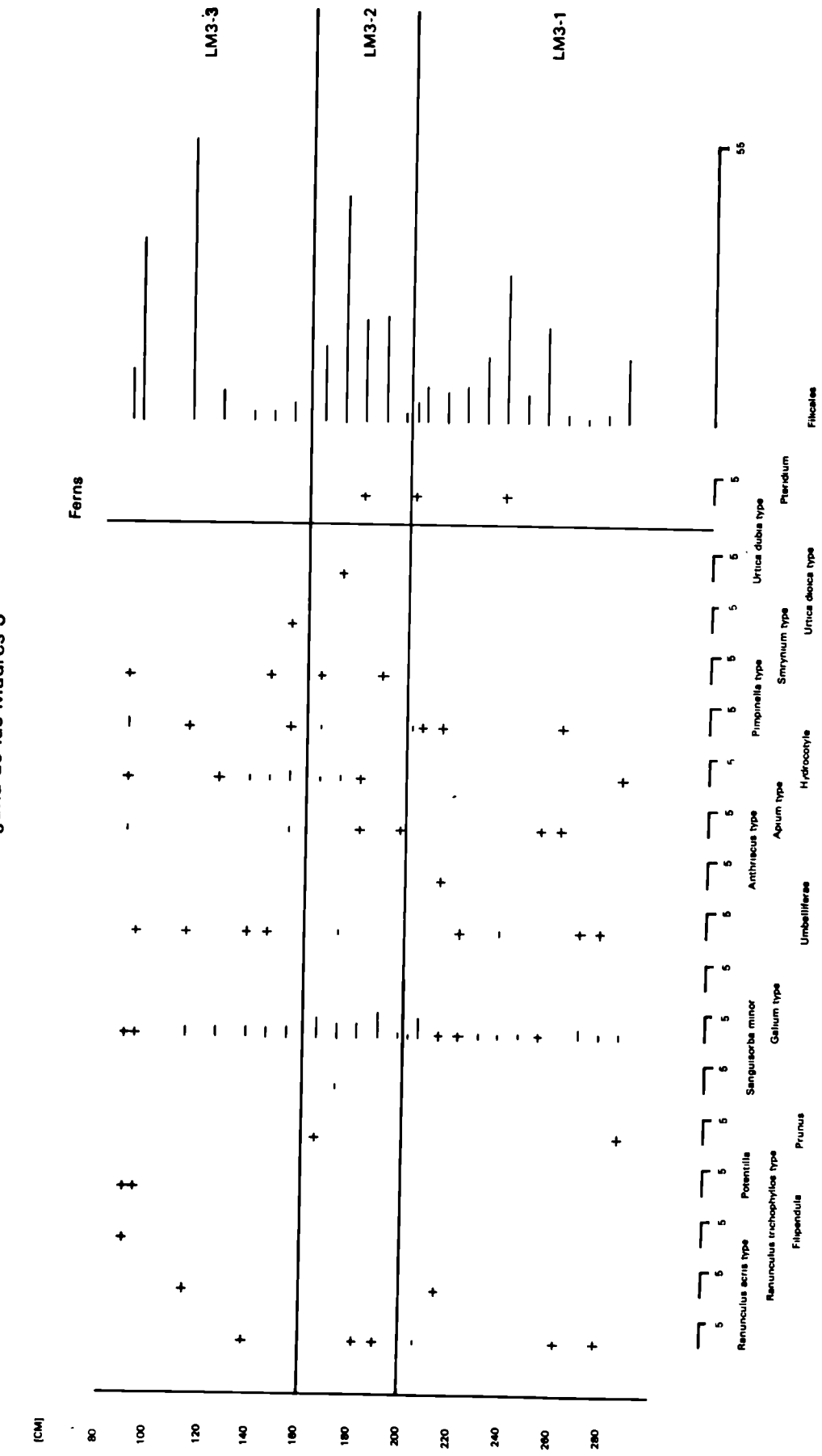

Laguna de las Madres 3
[CM]
80
100
120
140160
180
200
220
240
260
280
300
LM3-3
LM3-1
Gentiana
Erodium
Gramineae<40µ
Gramineae>40µ
Hypericum perforatum type
Asphodelus
Scilla type
Lythrum
Papilionaceae type A
Genista type
Lathyrus type
Lotus type
Melilotus type
Ononis baetica type
Plantago coronopus type
Plantago lanceolata type
Plantago major type
Rumex type

Fig.67


Laguna de las Madres 3
LM3-3
LM3-2
LM3-1
Ferns
[CM]
80
100
120
140
160
180
200
220
240
260
280
Ranunculus acris type
Potentilla
Ranunculus trichophyllus type
Filipendula
Prunus
Sanguisorba minor
Galium type
Umbelliferae
Anthriscus type
Apium type
Hydrocotyle
Pimpinella type
Smyrnium type
Urtica dioica type
Urtica dubia type
Pteridium
Filicales

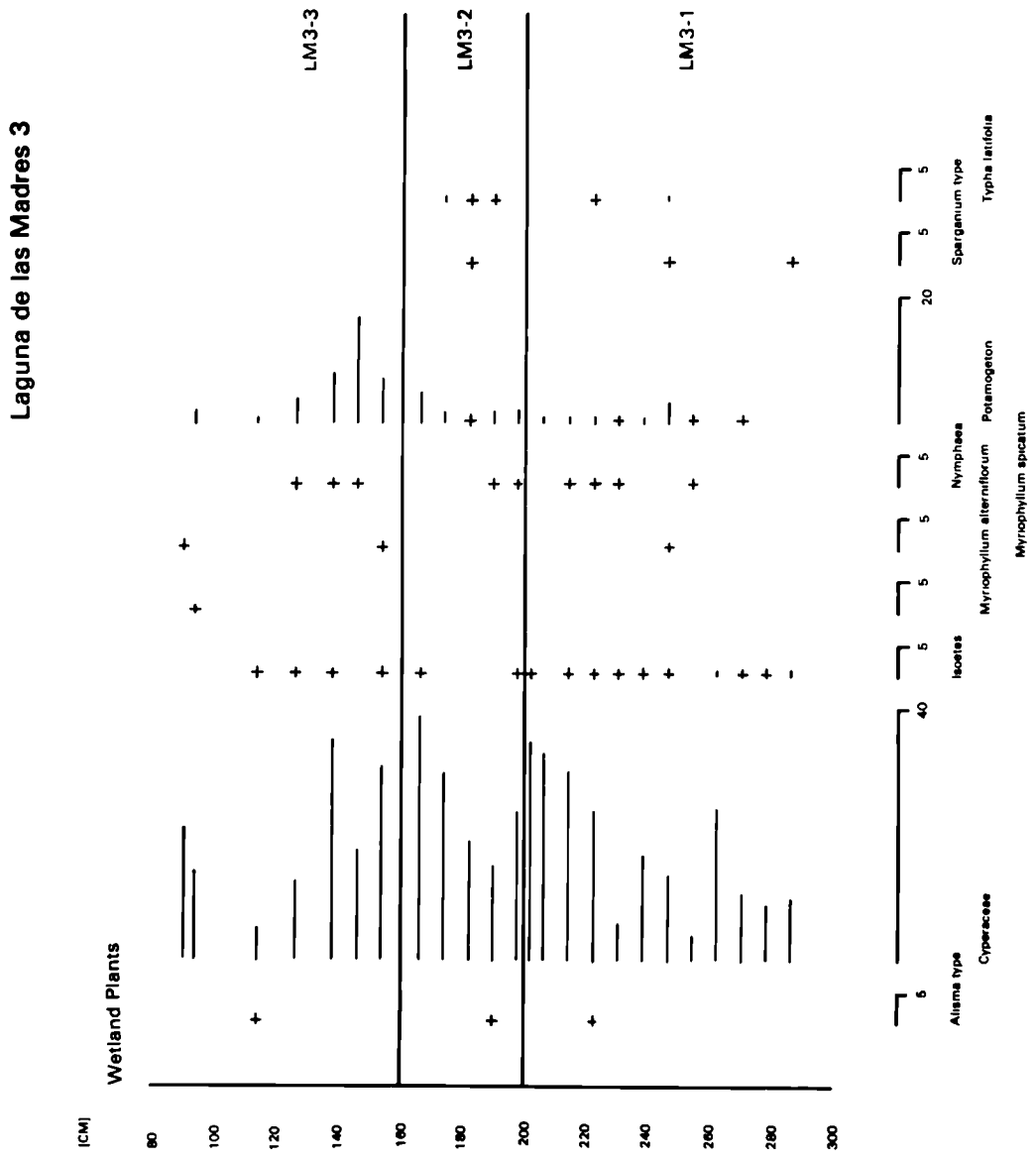

Laguna de las Madres 3
Wetland Plants
[CM]
80
100
120
140
160
180
200
220
240
260
280
300
LM3-3
LM3-2
LM3-1
Alisma type
Cyperaceae
Isoetes
Myriophyllum alterniflorum
Myriophyllum spicatum
Nymphaea
Potamogeton
Sparganium type
Typha latifolia
6
40
5
5
5
5
20
5
5

Fig.68

Pinus was being actively removed from the site at this time.

The shrub communities, however, expand midway through the zone, with peaks in Halimium type, Erica lusitanica type and Myrtus. The peak in Halimium type indicates the presence of monte blanco/negro shrub communities nearby. The peaks in these shrub types are correlated with a depression in Vitis. Two possible explanations of the depression in Vitis are :-

i) Poor pollen productivity at that time due to unfavourable weather conditions or insect predation.

ii) Abandonment of cultivation for a short period due to weather. disease or social disorganisation

The peak in Myrtus is the first time that this pollen type has appeared in any quantity. It is a shrub indicative of stable monte negro hygrophytic shrub vegetation and is correlated with the peak in E.lusitanica type and thus a general expansion of the shrub systems has occurred as a consequence of the disturbance of the vine population. Thus of the two possible causes the evidence favours the second explanation.

Thus the site was under heavy human influence in the form of viticulture, and obviously the date of this cultivation would be of upmost importance in determining which were the likely anthropogenic effects in the previous two cores.

Pollen Assemblage Zone LM3-2

Local

The local pollen assemblage sees an expansion in Gramineae, Galium type, Filicales, Cyperaceae and Potamogeton, which all appear to indicate an extension of swamp vegetation, with open pools conditions occurring at the end of this zone. Disturbance of the margins of the Laguna has also allowed Salix to peak

Regional

The striking characteristic of this zone is the complete disappearance of Vitis from the pollen record, save for one grain, and thus indicates the cessation of viticulture. However, the shrub and forest types do not respond, for Pinus continues to fall as do Halimium type and Erica lusitanica type values, which appear to be replaced by pastizal conditions as Rumex and Leguminosae pollen peak. Quercus values increase slightly in this zone but do not reach the high values seen in the previous two cores.

Pollen Assemblage Zone LM3-3

Local

Increasing wetness is a feature of this zone as indicated by the increasing values of Potamogeton, but by the end of the zone conditions have reverted to their original state with invasion by members of the Filicales.

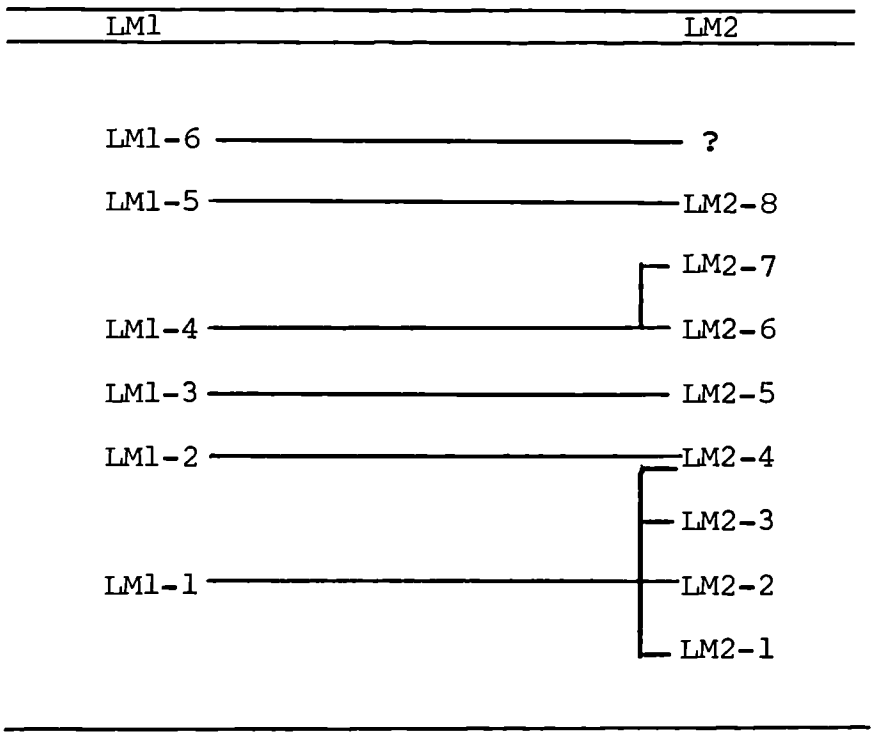
Regional

Quercus shows little fluctuation, but its values are still very low during this zone, whilst Pinus continues to fall gradually to low levels as well. The shrub types especially those dominated by Erica lusitanica type pollen recover, but the prominence of Halimium type seen in LM3-1 and indicative of monte blanco/negro shrub communities is not repeated.

Core Correlation and Dating of Cores

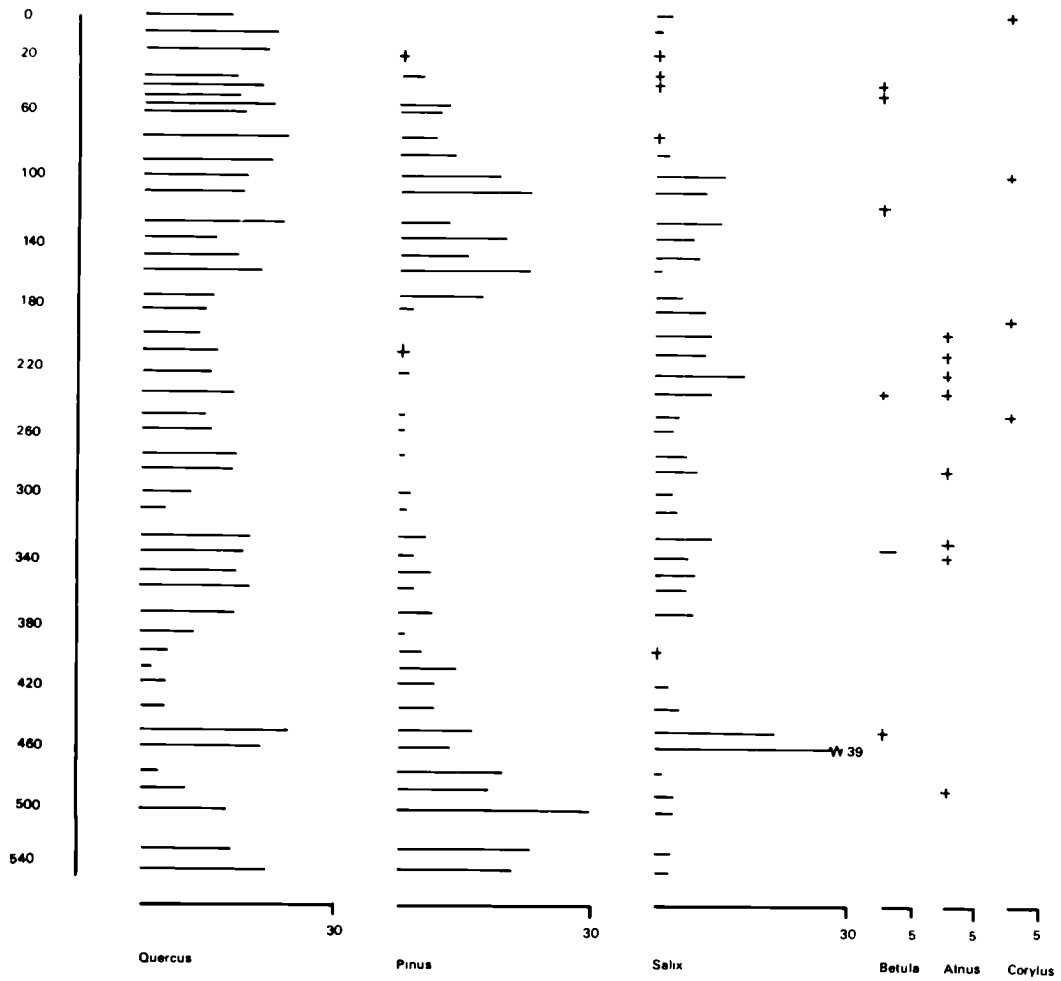
The easiest cores to cross correlate with one another are LM1 and LM2, since they present gross similarities in the pollen fluctuations in the diagrams, especially the tree components. A summary table of correlations is given below (Table 20)

TABLE 20



As can be seen from Table 20, zone LM1-1 contains all four bottom pollen zones from LM2, which is largely due to the pollen in the lacustrine sediments of LM1 being uncountable. It should be noted that peat initiation in the Laguna took place at different stages in both LM1 and LM2. It began at 194cm in LM1, where *Pinus* was high, and at 208cm in LM2 where *Pinus* was low. Thus peat formation in the Laguna was independent of the forest changes occurring.

Fig.69 Tree pollen diagram redrawn from Menendez Amor and Florschutz (1964)



Zone LM1-2 is correlated with the last portion of LM2-4 i.e. variable Pinus and the absence of a Salix peak. Zone LM1-3 and LM2-5 appear to be direct analogues i.e. high Juniperus peak and the absence of Pinus. LM1-4 correlates with LM2-6 and LM2-7 with the second Salix peak occurring, build up of Quercus to a peak and then its subsequent decline, and the build up of Pinus to its second peak. Zone LM1-5 correlates well with LM2-8, as the large Pinus decline occurs. Zone LM1-6 has no analogue(with low Pinus) and even since LM1 stops 20cm below the present day surface. Thus the top of LM2 almost certainly does not represent the present day surface and its pollen the modern day input into the Laguna.

A previous study of the site exists (Menendez Amor and Florschutz 1964), which possesses two radio-carbon dates. The tree diagram has been extracted from the published diagram of the site (Fig. 69), unfortunately it was not stated which pollen sum was used for the calculation of the data, though it is possible that some sort of land based pollen sum was used. There appears to be close similarities between the diagrams, i.e. Two Pinus peaks and two Salix peaks. A date of 4550 $\pm$ 75 b.p. was assigned to a point in their diagram where Salix peaks and Pinus declines. Of the possible events in LM2, LM2-2, LM2-4 and LM2-8 all qualify due to the falling Pinus values, from which it is possible to eliminate LM2-8 since it is too young and does not possess a Salix peak. Of the two remaining possibilities, Salix and Quercus are both absent from LM2-2, thus the closest analogue to the dated horizon in the diagram

of Menendez Amor and Florschutz (1964) is LM2-4. This event is not recorded from LM1, since it is contained in the non-polliniferous zone.

A date of 2220 ± 80 b.p. was given to a point in their diagram where Pinus was absent. It is only possible to identify a range in the present diagrams where this event takes place. In LM2, the event takes place between LM2-5 and LM2-6, whilst in LM1 it occurs between LM1-3 and LM1-4. In the dated diagram the date also precedes a Salix rise and a minor but continued influx of Alnus, thus it may be possible to place the date around 104 cm in LM2 and 132 cm in LM1. However, this may be an imprecise estimation due to the Salix peak in the dated diagram behaving somewhat differently from the present diagrams. Another point to stress is the large depth discrepancy between the dated diagram and those of the present. It is possible that peat disturbances have occurred in LM1 and LM2, for which evidence has already been indicated where LM1 finishes 20 cm below the surface but possesses a more complete record of recent events than LM2. It is reasonable to expect some peat loss from the surfaces that were bored, for the site was already being drained and the surface was very dry and thus a certain amount of peat may have been eroded away. In addition to this there is a depth discrepancy of 60 cm between events in the two diagrams, so it is not inconcievable that such a discrepancy is occurring between these and the dated diagram. It is known that peat growth is not uniform across a surface and LM1 and LM2 were nearer the edge than the dated core and therefore may have had

a lower rate of peat accumalation and thus LM1 and LM2 represent a condensed version of the dated core.

In comparing the dated diagram with the present ones, other discrepancies have been found :-

i) There is no evidence of high Chenopodiaceae input, thus the bottom of LM1 and LM2 appears to predate that of the dated core. Also no large input of Isoetes is recorded in the dated core, which further supports this argument.

ii) The large varia group would undoubtedly contain some important pollen types e.g. Juniperus and Phillyrea etc.

iii) Very little Nymphaea was found in the dated core but a major peak in Ilex was recorded from it. Since Ilex has never been recorded from this area and since the grains look superficially similar, it is likely that the Ilex records in the dated core refer to Nymphaea

iv) Sphagnum spores were found in the dated core, but Sphagnum is not recorded from the area and thus since its spores are very similar to those of Pteridium there may have been some confusion.

Correlation and Dating of LM3

This core is dealt with separately due to its potential importance regarding the indications of viticulture. It is difficult directly to compare LM3 with LM2 and LM1, since the tree values do not appear to follow the same distinctive patterns and also that the top 1 m of peat was not sampled due to heavy disturbance. However the falling *Pinus* values indicates three possible areas in LM2 where the cultivation of *Vitis* may have occurred :-

i) Decline in *Pinus* in LM2-2

ii) Decline in *Pinus* in LM2-4

iii) Decline in *Pinus* in LM2-8

Possibility three may be ruled out due to the event being too recent. Of the other two possibilities both of which are represented in LM2 but only the second in LM1, the low in *Quercus* found at the same time as the *Vitis* in LM3 would indicate possibility i) but, no evidence is recorded of a high Chenopodiaceae and Liguliflorae input at this stage. However, a grain of *Vitis* was found at 264 cm which is in concordance with this hypothesis. This grain could represent a natural population, but a major source of *Vitis* is suggested, for it has been shown how it is low in its pollen production and how poorly dispersed it is. Thus cultivation of *Vitis* may have occurred during this zone. Possibility ii) must however be considered. This event is

partially represented in LM1 and fully in LM2. Of great importance is the fact that grains of Vitis were recorded from the dated core at a depth of 425 - 450 cm, which postdates the Salix peak and is on a Pinus decline, and this stage was correlated with LM2-4. It is reasonable to assume that since Vitis is so seriously under-represented in naturally occurring populations, the occurrence of a continued input of Vitis albeit low, is indicative of large populations occurring nearby. Thus if a large source of Vitis was known to occur in the site, as seen in LM3-1, then it is reasonable to correlate the presence of a few grains with this source. Vitis was also recovered from LM1 at 160 cm, and this predates the first Juniperus rise

Assuming that the core correlations are correct and if the transfer of dates from one core to another is also correct, then one can assign a tentative date to the viticulture in LM3. If possibility i) was correct then the viticulture must predate 4550 b.p. and if possibility ii) then viticulture must have occurred between 4550 b.p. and 2220 b.p. The two possible date ranges for viticulture may not be exclusive since the Vitis record in LM2 was recorded from lacustrine sediments, which would accumalate very rapidly, especially since indications of heavy soil erosion are so evident during this phase. On the grounds of greatest evidence possibility ii) seems to be the most likely one, and thus provides some indirect evidence that the transfer of dates from the dated core to the undated core was also right.

Thus we now have a rough dating mechanism against which to base the forest changes and the occurrence of viticulture. With reference to Vitis, it had been thought that viticulture was introduced by the Romans (Way 1957), however the dates show that these records of viticulture predate the Roman invasion of the peninsula which occurred in 281 B.C. (G.Novo unpub.) . According to G. Novo (unpub.) the dates of viticulture correspond to Megalithic/Bronze age times and thus Bronze age cultivation of the vine is possible and Vitis cultivation may well have been associated with the establishment of Tartessus a major trading city that was situated in the mouth of the Guadalquivir (Menenteau 1981). It has also been noted that many of the words used in the wine-making process are not of Roman origin and are thought to predate the Romans (Vicente Martin personal communication). Viticulture appears to have ended abruptly around the birth of Christ.

When it comes to the correlation of events in the diagram with other historical periods, the situation is difficult due to the paucity of historical information about the Donana area. A climatic deterioration (i.e. drier conditions) was thought to have occurred around 500 B.C.(G. Novo unpub.) and may be correlated with the setback in Quercus and increase in Juniperus seen in LM2-5. However, this event may have had a tectonic origin, for a drop in the water table is all that is required to change the forest types. It is noticeable that a series of minor tectonic movements have affected the Guadalquivir in its lowest reaches (Menenteau 1981). At one time the river flowed directly into the sea and then

progressively gave way to a series of extensive meanders, whilst today the river once again flows direct into the sea, bypassing the meander system. Thus the imporatance of minor tectonic uplifting etc. must not be underestimated, since evidence for these processes is so strong along the coast.

Because the base of the diagram, dates to about 4550 b.p., the influence of man on the original Mediterranean forest has already been felt. So we have no way of telling whether the forest was once more extensive nor whether the forest recovered to something approaching the original condition. The Quercus forest did recover to a maximum at about 1770 b.p. after which it was progressively cleared. It is possible that its temporary recovery reflected the abandonment of agriculture developed under the pre-Roman and Roman civilisations, when Spain was invaded by the Visigoths in 400 A.D.. This situation lasted until the invasion of the Moors in 711 A.D. , who re-established agriculture in the region. The destruction of the forest seen in the second halves of the diagrams may reflect this re-imposition of agriculture on the natural vegetation. However, all these correlations remain speculative until independent dating of the cores can be implemanted.

Representation of the Different Community Types that can be Identified from Laguna de las Madres

Here will be discussed the actual community types that can be identified from the fossil pollen diagrams in Laguna de las Madres, by comparison with the modern pollen survey.

Monte blanco communities

The Juniperus values found in the Laguna diagrams are very high when compared with modern day sites (Cf Pu1, Pu2), the values suggest a dense Juniperus forest rather than scattered trees, since scattered populations of Juniperus are seriously under-represented.

The Pistacia communities do not appear to be a major feature of the pollen rain of the site. However, since Pistacia is under-represented and poorly dispersed, it is possible that such community types existed near the Laguna. The peak seen in LM1-5 may indicate an expansion of such a community.

The derived monte blanco shrub communities of drier soils are poorly represented in LM1 and LM2 save for an expansion of Halimium type pollen seen in LM1-6. This was to be expected since many of the shrubs of this system are seriously under-represented in the pollen rain e.g. Genista anglica and Rosmarinus officinalis. The high values of Halimium type pollen recovered from LM1-6 shows that indications of such a community type can occur but for most of the two main cores LM1 and LM2 monte blanco communities were scarce near the site. It is interesting to note that

the disturbances of the monte blanco forests do not lead to the development of the derived shrub vegetation.

Monte negro communities

The Olea community is poorly represented in the pollen input but this reflects the results of the modern pollen survey, where it was found that Olea is a good pollen producer but is poorly dispersed.

The derived monte negro shrub communities are likewise poorly represented, but as seen in the modern pollen studies it is impossible to distinguish them from monte blanco shrub communities.

Monte negro hygrophytic communities

The forest communities of this type, dominated by Quercus, are well represented in the pollen rain. However, certain of the shrubs that are understorey components in the forest e.g. Arbutus,are under-represented. This tree has a low pollen productivity like many of the Ericaceae and is also poorly dispersed, mainly because it discharges pollen into the trunk space of Quercus forest, where lianas reduce wind movement through the trunk space and hence prevent its export from the community. This also applies to Phillyrea, however, the extent of the liana population cannot be estimated for the major liana component, Smilax is seriously under-represented in the pollen rain.

The derived shrub communities of this forest type are well represented in the pollen rain of the Laguna, featuring prominently in some of the perturbation phases of the Quercus forest. Phillyrea input is normally high when this shrub type is extensive, which is due to its discharging pollen into the canopy region rather than the trunk space of the forest's stratified structure.

Fraxinus/Tamarix communities

Evidence for the existence of these communities is poor; there is an input of Fraxinus pollen, but it is irregular and low. Thus the contribution of Fraxinus/Tamarix to the vegetation cannot be determined.

Mobile sand dune communities

Evidence for this community type is high, as indicated by the large amount of Pinus recorded. However, it cannot be differentiated from disturbance around the edges of the Laguna or from extensive plantings of the tree.

Thus it appears that the vegetation types that can be detected in the modern pollen survey, on the whole can be detected in the fossil pollen assemblages and provide a reasonable basis for the interpretation of the diagrams. Of the vegetation types with no direct analogues seen in the modern pollen survey only one is of major importance, that of the high Chenopodiaceae/Liguliflorae inputs found in the

base of LM1 and LM2. The other types not found are the aquatic communities which were not sampled in the modern pollen survey.

CHAPTER FIVE

Encinillas Altas

The core was taken from within the Doñana National Park at a site, which is covered by what has been thought to be a remnant of the original Quercus suber forest, a forest type that is considered by some to have covered the reserve before the activities of man. The aim of the analysis was therefore,to try to ascertain if the forest was indeed a remnant of the original Mediterranean forest and if not what was its origin.

Methods

A pit was dug in the centre of a mature stand of Q. suber trees, with an understorey of Phillyrea angustifolia and Arbutus unedo and a ground cover of Pteridium aquilinum (for a more detailed vegetation list refer to the modern pollen survey samples D100-105 and D7). The depth of the pit was approximately one metre and the rough stratigraphy is shown in Table 21. Samples were removed from the pit every 5 cm using a clean knife blade and all efforts were taken to ensure there was no contamination. The samples were transferred to clean sealable polythene bags for transport back to London by air, where they were stored in the dark at 2°C until required for analysis.

The preparation of the samples was as set out in Appendix B, the HF stage being three hours. The samples were mounted on

TABLE 21

Encinillas Altas :- Stratigraphy

Depth cm	Description
0-20	Leaf litter and decomposing humus
20-92	Organic sand

TABLE 22

ENCINILLAS ALTAS 1

Zone	Pollen Assemblage Zone	Types Diagnostic of Zone
EA-4	*Quercus*-*Arbutus*-*Phillyrea*	*Quercus* increases steeply, *Arbutus* and *Phillyrea* increase, *Halimium*, *Erica* and Gramineae all fall.
EA-3	*Halimium*-*Erica*-*Quercus*	*Quercus* increases, *Halimium* high, *Erica* high, *Mentha* high
EA-2	*Halimium* *Erica*-*Pinus*	*Quercus* peak, *Pinus* falls, *Halimium* high, *Erica* high
EA-1	*Pinus*-*Halimium*-*Erica*	*Pinus* falls, *Halimium* high, *Erica* peaks

Encinillas Altas 1

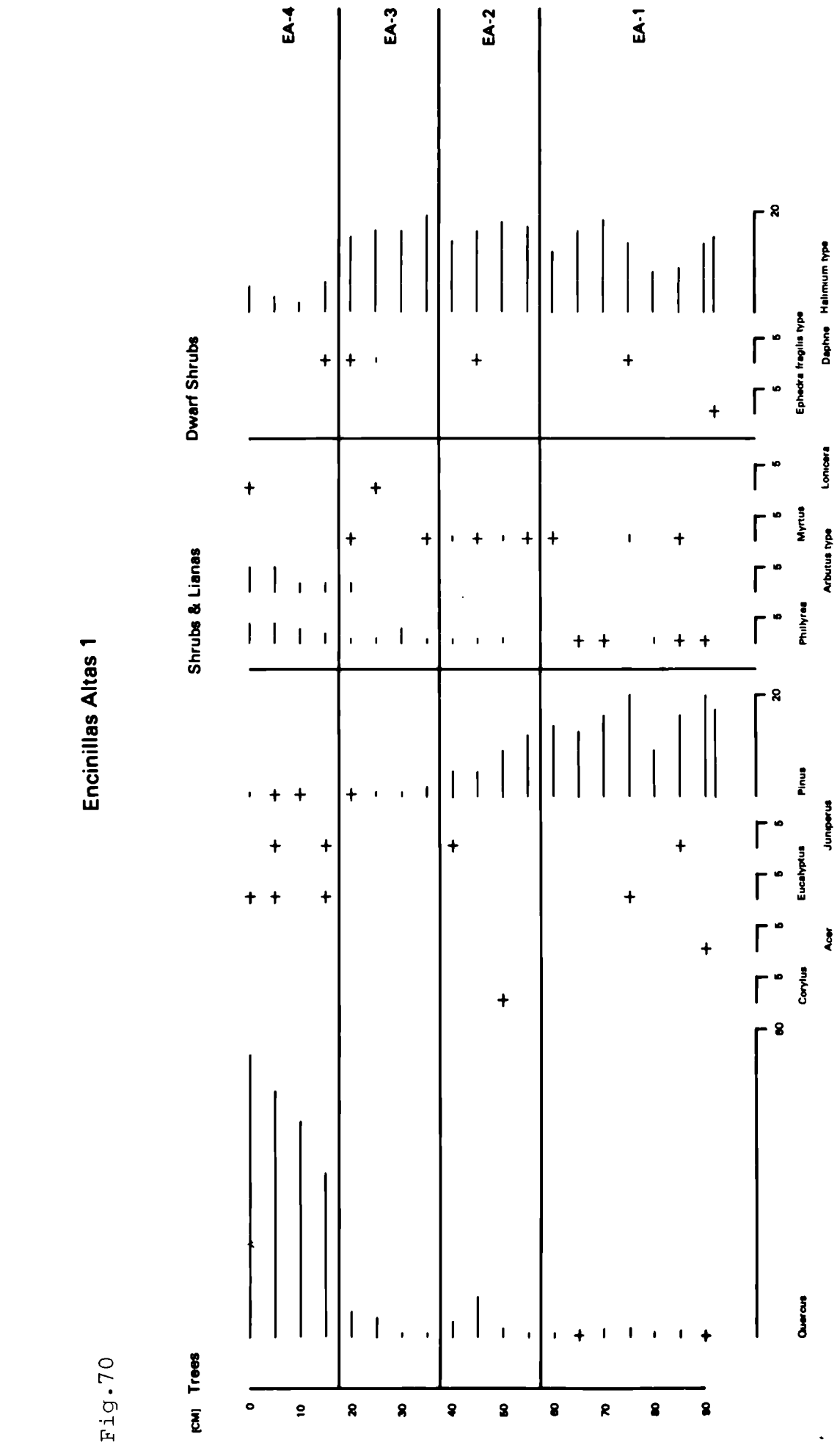


Fig.70

Fig.71

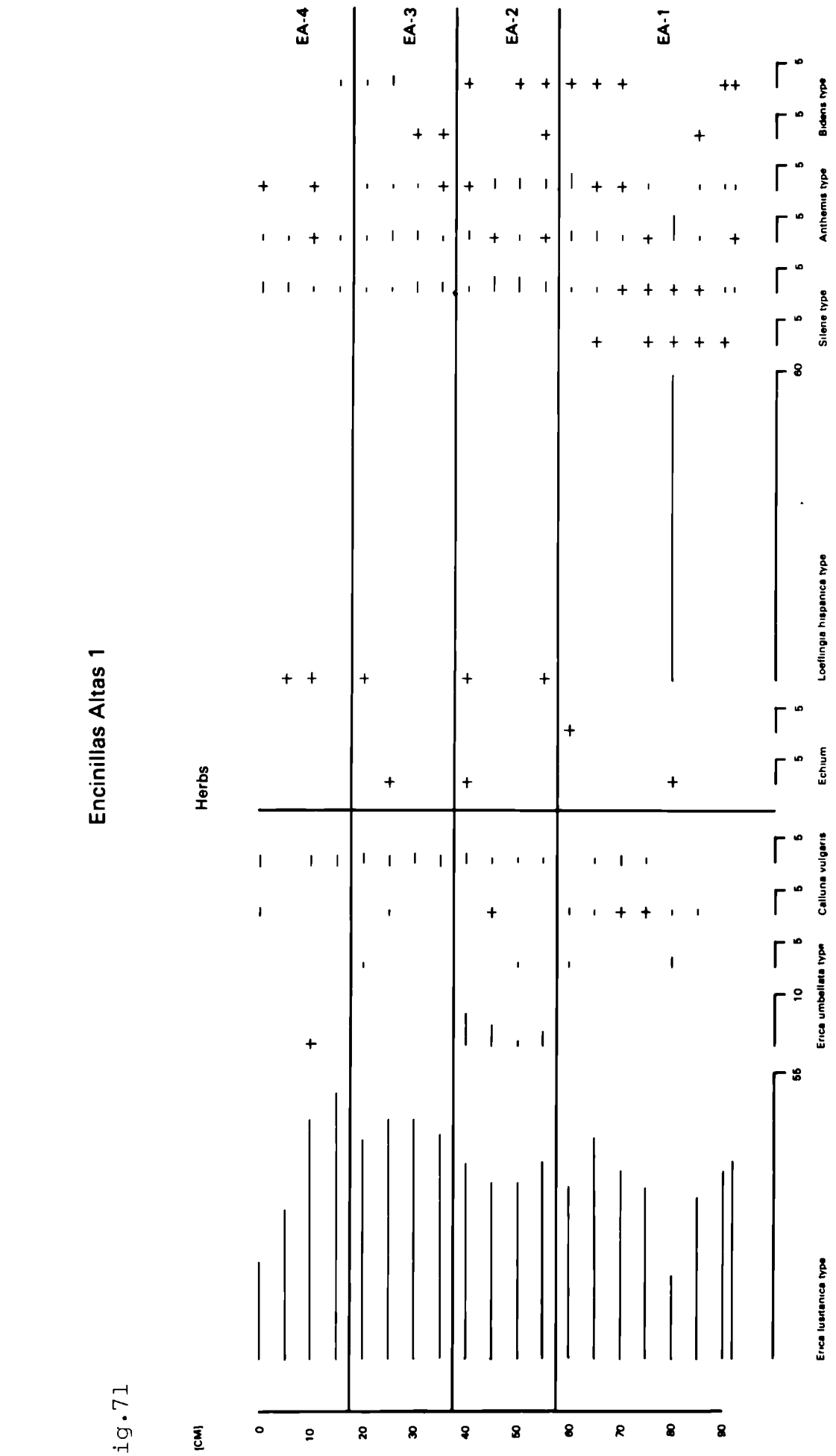

Encinillas Altas 1
Herbs
(CM)
0
10
20
30
40
50
60
70
80
90
EA-4
EA-3
EA-2
EA-1
Erica lusitanica type
Erica umbellata type
Calluna vulgaris
Erica vagans type
Mentha type
Echium
Caryophyllaceae
Loeflingia hispanica type
Silene type
Anthemis type
Bidens type

Fig.72

Encinillas Altas 1

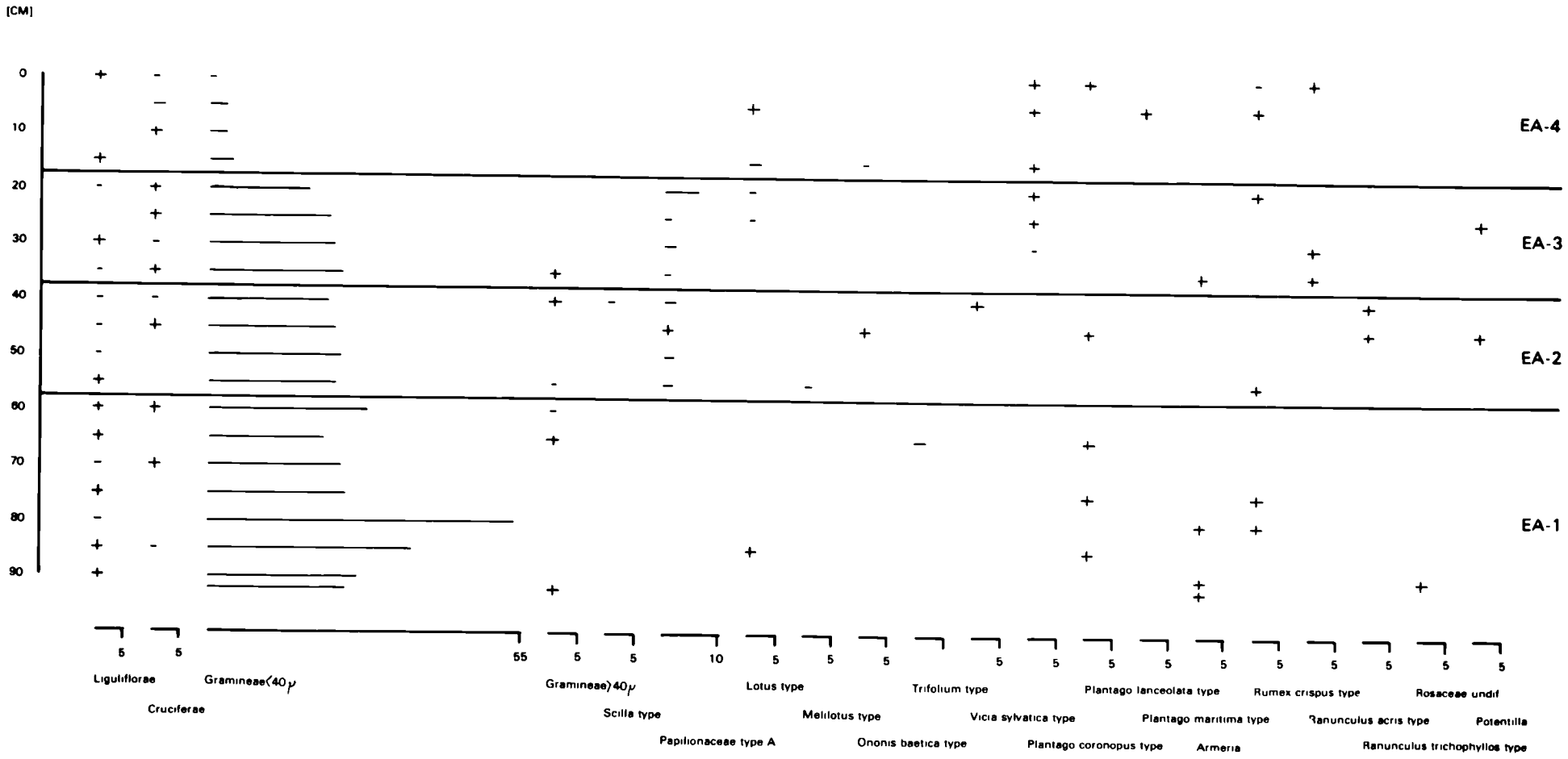
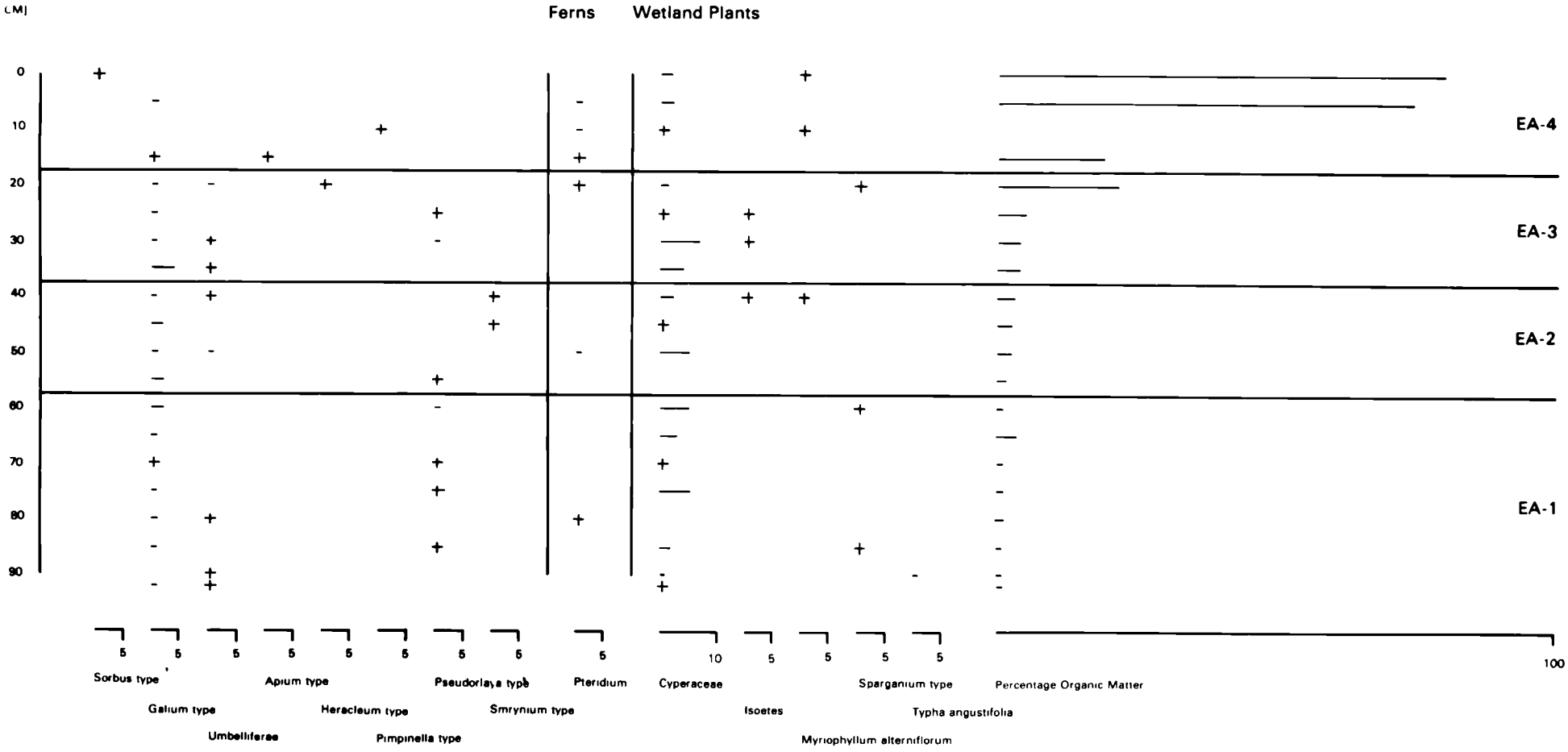


Fig.73

Encinillas Altas 1



duplicate slides and a total pollen count of 500 pollen was made from each level, excluding Loeflingia and Cyperaceae. Pollen identification follows Moore and Webb (1978) and types not given there will be found in Appendix A.

The samples were also subjected to organic matter determination by burning oven dried samples in a muffle furnace at 650°C. The results of this analysis are shown in the accompanying pollen diagrams.

The pollen diagrams have been divided into broad life form groupings as before (see p203). The pollen sum used to express the majority of the pollen types was :- Total pollen minus Cyperaceae and Loeflingia. The percentages of both Loeflingia and Cyperaceae were calculated on the basis of the total pollen.

The pollen diagrams are given in Figs. 70-73, and have been zoned conventionally, the basis of which is given in Table 22

Interpretation

Pollen Assemblage Zone EA-1

In order to find the type of plant community responsible for the pollen rain at this time, it is necessary to compare the fossil pollen rain with that of the modern pollen rain of many of the Mediterranean communities. The high Halimium type values and the presence of Mentha type and the relatively low input of Erica lusitanica type all indicate the presence of a monte blanco/monte negro shrub community. The higher values of E. lusitanica type may indicate a monte negro rather than monte blanco community but depends on the spatial patterning of the different communities. The monte blanco/negro shrub communities being indistinguishable on the basis of their pollen rain (p 125).

Soils during this phase appear to be disturbed, low values of Phillyrea and high values of Gramineae and Loeflingia and Pinus all indicate a degree of instability of the soils and this may be the reason why Juniperus does not achieve significant inputs. The Pinus peaks may however, have an anthropogenic cause, a point that is discussed later on in the chapter. Thus the site at this time resembles a monte blanco/negro shrub community with evidence of soil disturbance. This may have been caused by the vegetation still experiencing the activities of the mobile sand dunes, for ultimately the vegetation has developed on a system of dunes and slacks that have stabilised (G.Novo 1979).

Since the site at this time consisted of a monte blanco/ negro shrub community, one would expect a heavy non-local

input of pollen to occur, due to the openness of the community and consequent lack of filtration, a process that happens in the equivalent sites today. The input of Quercus is roughly equivalent to that of today and is suggestive of a Quercus population that is low. The Pinus populations appear to have been higher, with inputs far in excess of those of the present day.

The development of the vegetation during this zone undergoes three different phases :-

i) Pinus falls, Halimium falls, Erica lusitanica type falls, Gramineae rise and a peak in Loeflingia

ii) Pinus recovers but falls again, Halimium type rises Erica lusitanica type rises and Gramineae fall.

iii) Pinus rises, Halimium type falls , E. lusitanica type falls and Gramineae rises.

Phase i) indicates great disturbance culminating in the development of almost complete dominance locally by Loeflingia, a plant that is characteristic of dry unstable sand surfaces. The Gramineae also increase during this phase again indicative of the replacement of shrub by open grassland. The falls in Pinus etc. may have been caused by a proportional effect of the Gramineae rise.

Phase ii) sees a steep fall in the Gramineae and Pinus recovers immediately only to fall once more, the rise being

a proportional effect. The monte blanco/negro shrub community increases slowly during this phase, indicating the recolonisation of the soils previously dominated by Loeflingia. Phase iii) sees Pinus values continue to fall, which indicates the removal of the tree from the locality. Possible causes of the decline are :-

i) Changing water tables, but no evidence is seen for stabilisation as would be indicated by expanding Juniperus, nor is there any evidence for replacement by other forest types.

ii) Anthropogenic effects, a feature that will be discussed later, for it is this explanation that is the most likely.

Pollen Assemblage Zone EA-2

This zone is characterised by declining Pinus values, which fall to values that approximate todays input into the equivalent sites. The monte blanco/negro shrub community does not appear to undergo any drastic changes during this zone. A peak in the Chenopodiaceae values that occurs here may indicate some soil disturbance in the area, specifically associated with agricultural practices that were known to occur in the Park (G.Novo 1977) e.g. slash and burn cultivation of Hordeum , but no appreciable increases in Gramineae values are recorded. The fall in Pinus during this zone has been a continuing process since the previous zone, the cause of which is likely to have had an anthropogenic

origin.

Of particular interest is a peak in Quercus before the end of the zone, which suggests that Quercus must have been quite near at this time (Cf D104,D105). However, the peak is not sustained and falls away again to its previous levels.

Pollen Assemblage Zone EA-3

The shrub pollen types again do not change dramatically during this zone and are indicative of stable conditions. However, the tree communities do change with Pinus now almost disappearing from the pollen record, with inputs lower than those seen in the equivalent sites today and thus is suggestive of almost complete removal of Pinus from the area. Quercus however, after remaining low for most of the zone, even after the disappearance of Pinus now begins to increase, a process that is carried on into the next zone. The cause of the Quercus increase cannot be established; conditions have been quite stable throughout the diagram and possibly Quercus needs very stable conditions before it can invade. If an anthropogenic cause is postulated for the Pinus removal then Quercus may have been the subject of such effects. The invasion of Phillyrea would tend to indicate the stability theory for the Quercus invasion as would the first appearance of Arbutus.

Pollen Assemblage Zone EA-4

The shrub communities in this zone undergo a distinct change which is associated with a steep rise in *Quercus*. The *Quercus* rise now indicates the presence of mature trees growing on the site and forming a closed canopy, which would oust all the shade intolerant shrub community plants. Associated with the rise in *Quercus*, peaks in *Phillyrea* and *Arbutus* also occur, both trees being very common understories in *Quercus* forest. The pollen input of *Arbutus* is an under-representation of its importance, but the relatively high values found here indicate a local canopy.

The present day woodland contains a dense liana population, chiefly *Smilax aspera* , but *Lonicera* also occurs, however, these do not figure in the pollen rain except for one grain of *Lonicera*.

Age of Encinillas Altas

The age of this site is of great interest for it has been thought to represent the last surviving remnant of the original Mediterranean forest that once covered the Park.

The stabilised sands on which Encinillas Altas stands, has its origin geologically in a coastal plain that originated in the Pliocene (I.G.M.E. 1975). Within the boundaries of the Park, it is covered by sand dunes in which seven successive phases are recognised (Pou 1976),which all originate under the influence of west or south west winds. The dunes are parabolic (Chapman 1976) or transgressive (Davies 1972) and present day topography shows a series of arched ridges (old dunes) 0.5-2.0 km long and 100-200 m wide, separated by flat depressions (the old slacks). A fairly shallow water table results in frequent flooding of the depressions to give temporary ponds and lagoons, for the drainage network is poorly developed and functions only after heavy rains. All the dunes have been fixed long ago (G.Novo 1979) and no sand movement takes place at present.

The recent history of the Park from the 16th century onwards is relatively well known. The area was used as a hunting reserve for many years by the Dukes of Mendina Sindona, before the estate was bought by W. Garvey in 1901 and subsequently by the Duke of Tarija in 1914. In 1928 the estate was divided and the northern 2/3 passed to a syndicate headed by Marques del Merito, while the southern portion passed to the Marques de Borghetto. Following expeditions

to Donana in 1952,1956 and 1957 (Mountfort 1968), the World Wildlife Fund and the Spanish government purchased 7,500 ha, the Park has subsequently been extended and today comprises 49,000 ha.

The first historical record of the trees of the Park are found in the early 17th century, and 7,000 Quercus suber trees were counted (Granados Corona 1980) in a census of the Park. Pinus trees were, however, not recorded in the census, which implies the absence of the tree since it is commercially valuable. Pinus is not recorded until the census's of 1770 and 1774 (Granados Corona 1980). It is known that in the 1750's the mobile sand dunes became very active and swamped the Park, presumably killing most of the Quercus suber growing there. The dunes are known to have reached 30 km inland (Granados Corona personal communication). Intensive management of the Park has occurred since the 18th century and included game shooting, shifting cultivation, lumbering(Pinus and Juniperus), charcoal burning, cork and Pinus cone collection, cattle introduction and fire (G.Novo 1977).

The stratigraphy of the diagram until 20 cm consists of organic sands. A similar site has been found under monte negro hygrophytic vegetation (Doñana Pit) and has taken approximately 100 years to build up the same amount of sand. The accretion rate of sand would be expected to be high, thus the time taken for the bottom 2/3 of the core to be laid down will have been quite short in comparison to the top 20 cm of the core that consists of leaf material whose

accumalation rates would have been a lot slower.

The Pinus domination at the base of the diagram would seem to point to an initial age therefore of post 1750, especially with the evidence of the mobile sand dune activity. However, it must be remembered that Pinus has been found in deposits older than this i.e. Asperillo and Laguna de las Madres. The low Quercus values at the bottom of the core would indicate the absence of the tree from large areas of the Park. This is in agreement if the sands had destroyed a large population of Quercus, leaving very few trees to produce an input into the site. The instability found in EA-1 may be the final results of this mobile sand dune activity. The recovery of Eucalyptus pollen from this zone further enhances a recent origin of the core, unless comtamination has occurred.

The vegetation now changes very little except for the continuing fall in Pinus which was probably logged (Granados Corona 1980) until the steep rise in Quercus, for which there are two possible reasons :-

i) Normal Quercus succession into monte blanco/negro shrub communities. The mere fact that Quercus is growing there indicates a monte negro vegetation rather than a monte blanco one at this stage, since the water tables are too deep in monte blanco communities. A change in the water tables may have made the community more susceptible to invasion by Quercus

ii) The deliberate introduction of Quercus by man. It is known that vast plantations of Q. suber were made in Portugal and Spain in the early 19th century (Way 1957) for cork production. The fact that a gap occurred in the diagram between the final reduction of Pinus to low levels and the beginning of the Quercus increase could indicate active discouragement of Pinus and the introduction of Quercus, the lag phase being due to the time taken for Quercus to reach maturity. However, the pollen record also reveals a build up of Arbutus and Phillyrea at the same time; if Quercus were being used for cork production then an understorey would be undesirable, and would have been prevented from growing.

Thus the evidence appears to point to recent development of Q. suber forest, possibly by normal successional processes after invasion of the monte negro shrub community which had colonised the sands once they were stable enough.

It is impossible, however, to come to any conclusions about the development of forest in the rest of the Park, since the site in EA-4 records only the local pollen of this site. Thus since the site has changed from an open structure, with low filtration of incoming pollen, to one with a dense canopy and thus greater filtration of imported pollen, then vegetation changes in the rest of the Park cannot be elucidated. Changes have undoubtedly occurred in the vegetation of the Park, for documents refer to extensive removal of Pinus in 1901 and subsequent reintroduction in 1914 (Granados

Corona 1980). Fire and excessive pastoral practices as well as dune dynamics have been thought to have played a major role in the diminution of the original forest which is considered to have been dominated by Quercus faginea/Olea, and which was progressively fired to Q. suber / Arbutus (G.Novo 1977). But the importance of these factors cannot be ascertained from this site, however, it is clear that the bottom of the diagram reveals a situation very similar to that of today in terms of tree populations and thus sites must be found that will give an older perspective to the forests of the Doñana National Park.

Doñana Pit

This site was the second one to be examined in the Doñana National Park. A soil pit was excavated from beneath a stand of monte negro hygrophytic shrub vegetation and samples were taken every 2 cm and transferred to clean, sealable polythene bags for transport back to London, where they were stored in the dark at 2°C until required for analysis. Preparation of the samples was as given for the samples from Encinillas Altas. 500 pollen grains excluding Ericaceae and Cyperaceae were counted from each level. The resultant pollen diagrams are given in Figs. 74-77. All the types apart from the Ericaceae are expressed as a percentage of the total pollen minus the Ericaceae, which themselves were expressed as a percentage of the Total pollen.

The site represents development of vegetation since the abandonment of agriculture approximately 100 years ago. Today the site is a prime example of stable monte negro hygrophytic shrub vegetation, dominated by Erica scoparia and Erianthus ravennae. A full vegetation description will be found by referring to the vegetation records of Dh4 surface sample, which was taken nearby.

Despite the short timescale of the core, several interesting points can be made about the vegetation succession seen in the diagram :-

i) The site has borne monte negro hygrophytic vegetation

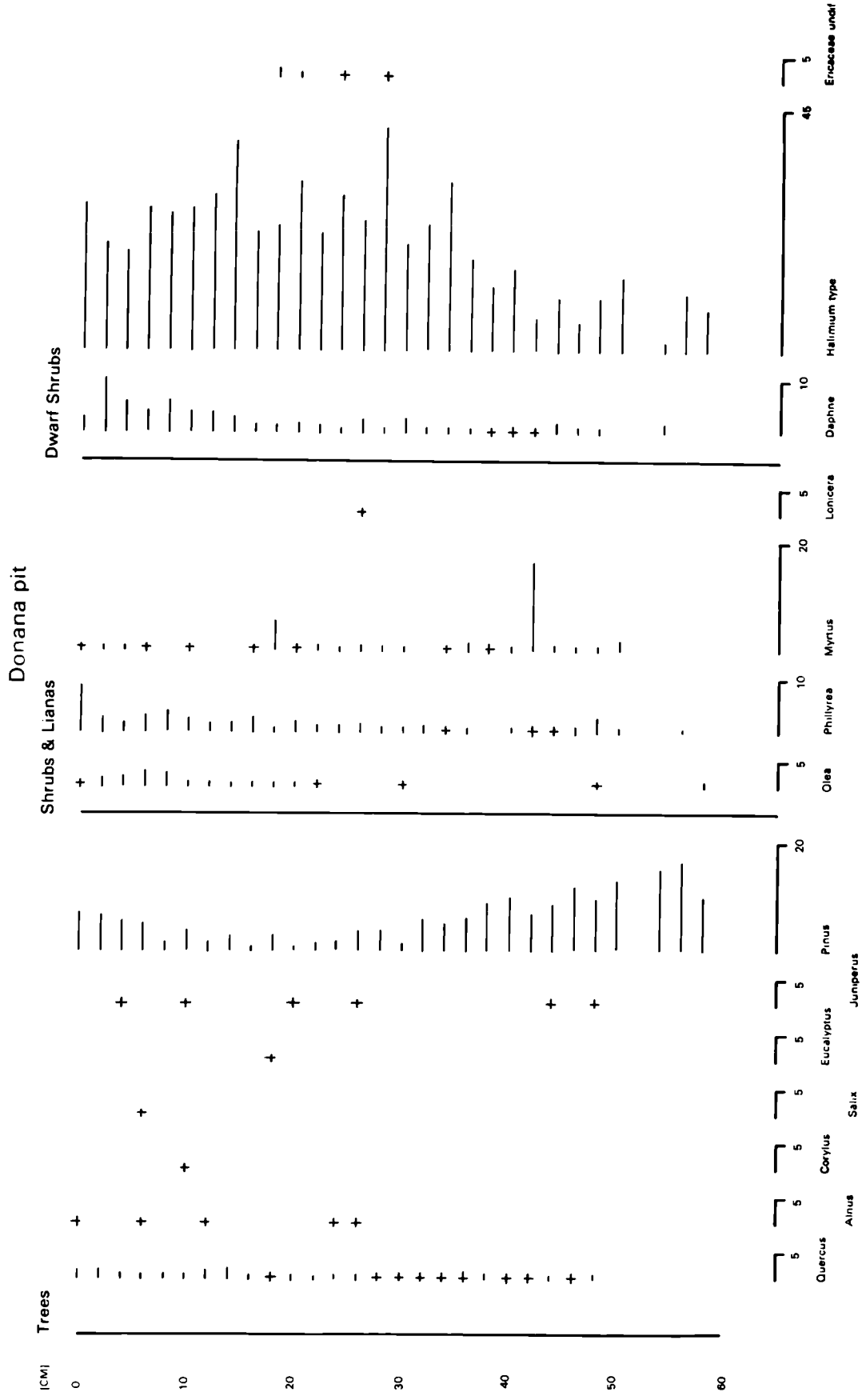

Donana pit
Trees
Shrubs & Lianas
Dwarf Shrubs
(CM)
0
10
20
30
40
50
60
Quercus
Alnus
Corylus
Salix
Eucalyptus
Pinus
Juniperus
Olea
Phillyrea
Myrtus
Lonicera
Daphne
Halimium type
Ericaceae undif

Fig.74

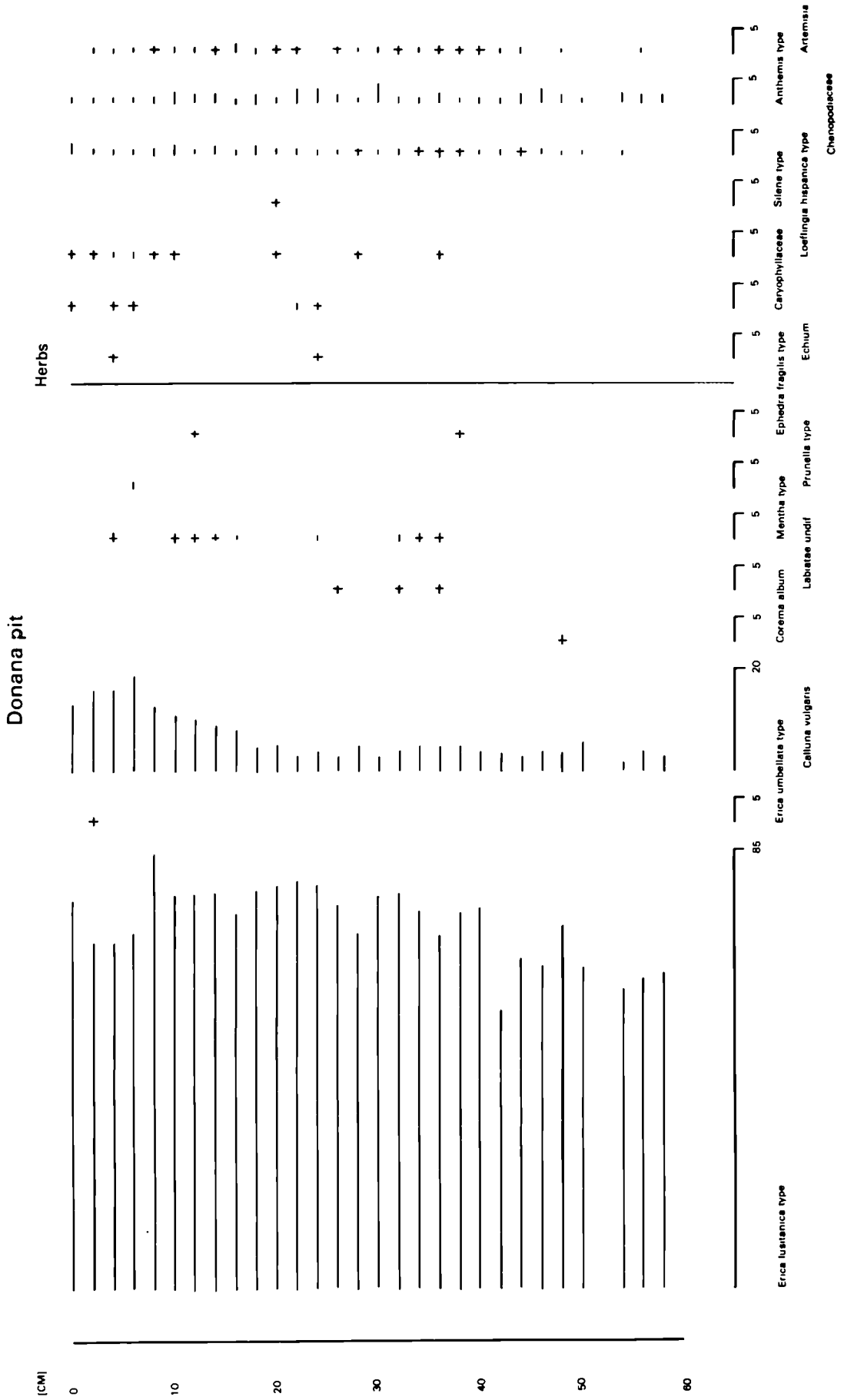

Donana pit
Herbs
(CM)
0
10
20
30
40
50
60
Erica lusitanica type
Erica umbellata type
Calluna vulgaris
Corema album
Labiatae undif
Mentha type
Prunella type
Ephedra fragilis type
Echium
Caryophyllaceae
Silene type
Loeflingia hispanica type
Anthemis type
Artemisia
Chenopodiaceae

Fig. 7.3

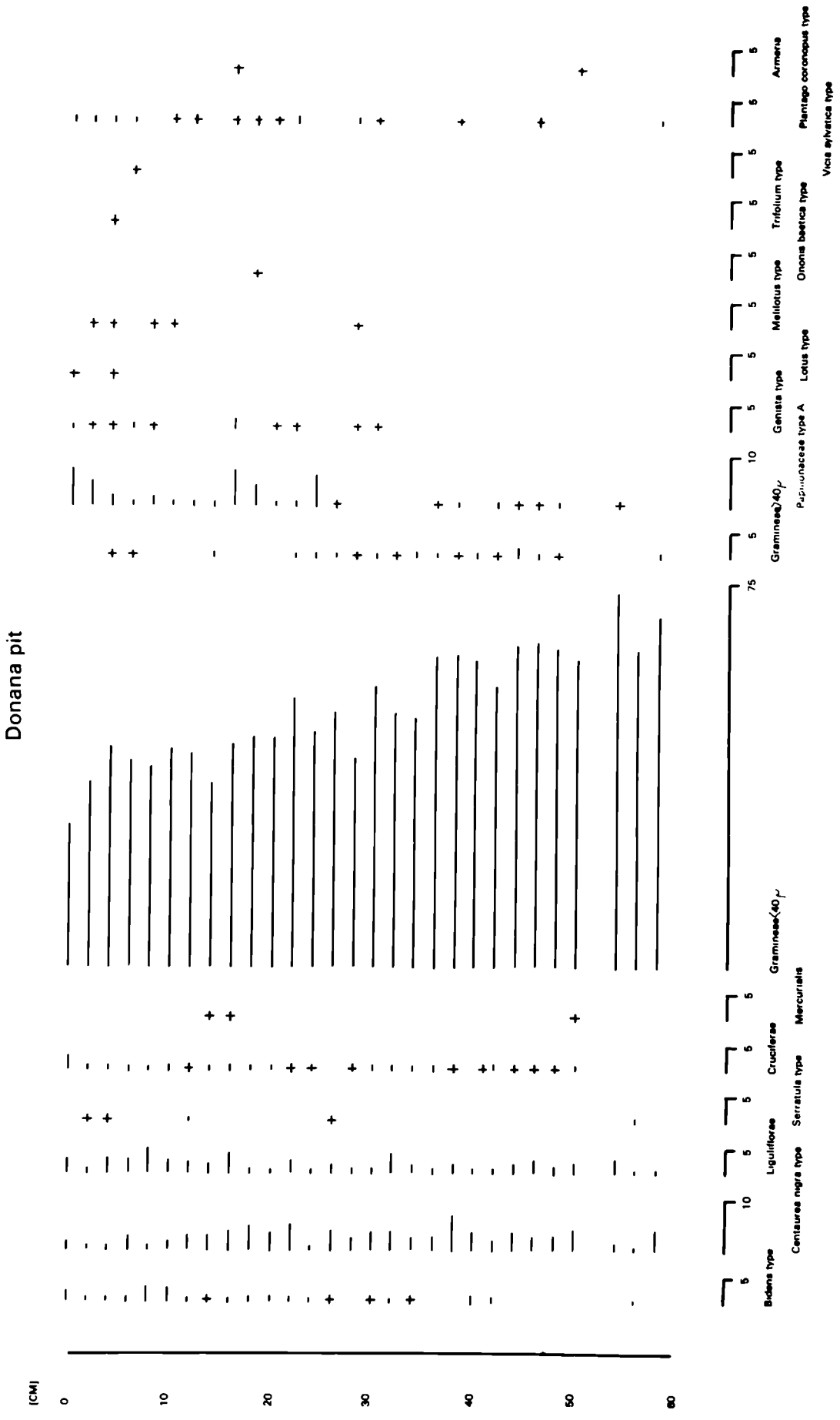

Donana pit
(CM)
0
10
20
30
40
50
60
Bidens type
Centaurea nigra type
Liguliflorae
Serratula type
Cruciferae
Mercurialis
Gramineae<40μ
Gramineae>40μ
Papilionaceae type A
Genista type
Lotus type
Medicago type
Onobrychis type
Trifolium type
Vicia sylvatica type
Armeria
Plantago coronopus type

Fig.76

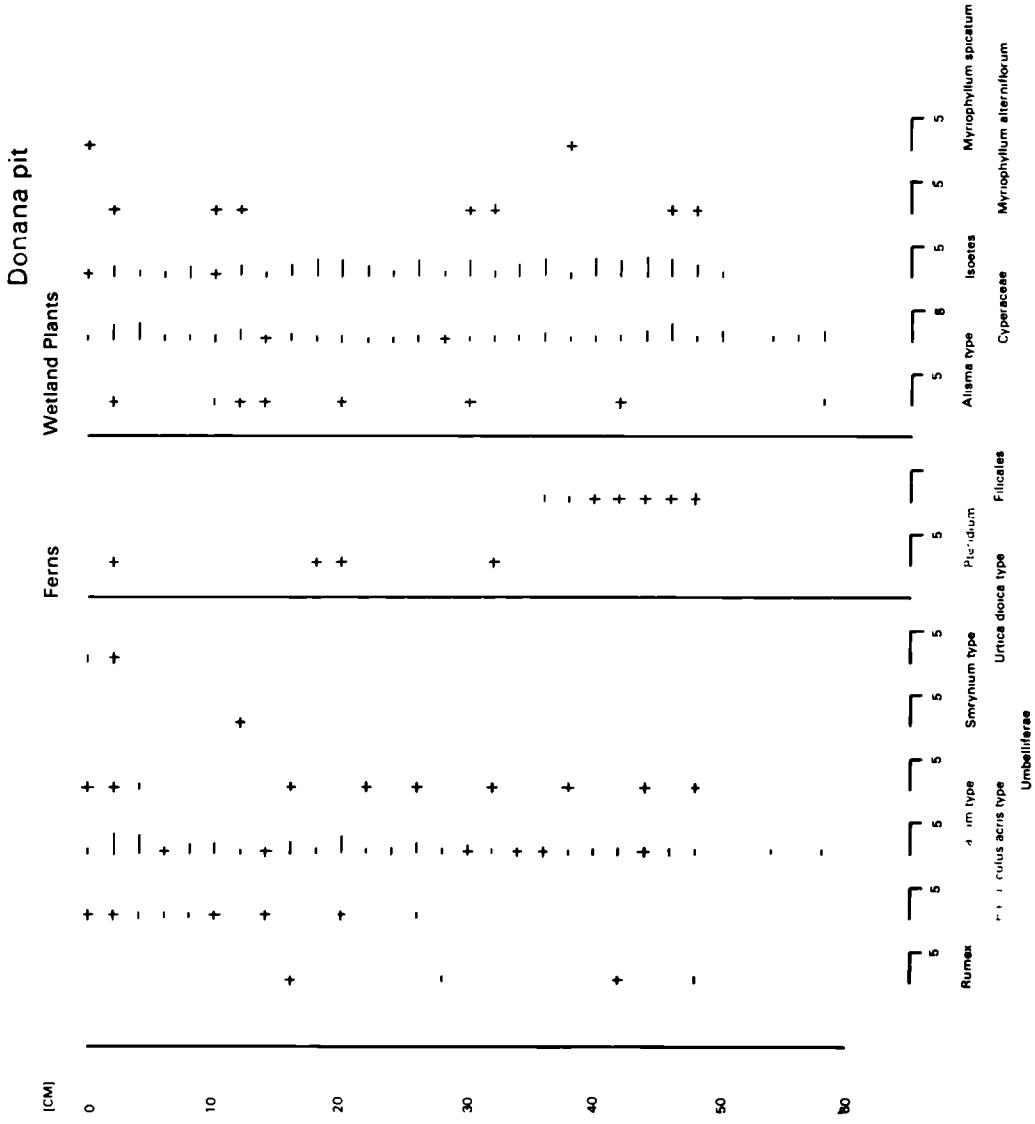

Donana pit
Wetland Plants
Ferns
(CM)
0
10
20
30
40
50
60
Rumex
Smrynium type
Urtica dioica type
Filicales
Alisma type
Isoetes
Cyperaceae
Myriophyllum alterniflorum
Myriophyllum spicatum
Umbelliferae

Fig.77

throughout the record of the core, despite the presence of large Halimium type values (which is in part a consequence of the pollen sum used which excludes the Ericaceae)

ii) There is increasing Quercus representation towards the surface, which is interesting for Quercus is very scarce in the Park at present. However, the low values of pollen recovered from the bottom of the core may be a reflection of differential degradation rather than increasing Quercus.

iii) There is a decrease in Pinus followed by an increase. The decrease seen in the first half of the diagram probably refects logging of this tree in the period 1900-1910 (Granados Corona 1980) and the subsequent reintroduction in 1940 is reflected in the subsequent rise in Pinus values seen.

iv) The Olea representation is also high compared to the modern day pollen survey but once again this may be a feature of the pollen sum used in the diagram. The increase in Phillyrea seen in the diagram is evidence of the increasing stability of the shrub system and it appears that 100 years are needed for this process to occur. The values Phillyrea are low when expressed as a percentage of the total pollen and is comparable to results obtained from the modern pollen survey of monte negro hygrophytic shrub vegetation, where Phillyrea

pollen is discharged into a canopy component of pollen flow and must be imported into the site of deposition, during which the pollen suffers heavy filtration.

v) The peaks in Myrtus undoubtedly indicate the local presence of the plant, and indicates that Myrtus can be very productive in pollen but it is poorly dispersed, which is probably a feature of it discharging its pollen into a trunk space component which in monte negro hygrophytic communities does not tend to lead to export of any pollen.

vi) The rising Daphne and Halimium type values seen in the diagram are interesting for, although Daphne may be r garded as evidence for stability in the same way as Phillyrea, it is known that both Daphne and Halimium type respond to fire (G.Novo 1977). Daphne is able to resist fire whilst Halimium invades by seed very quickly and in great numbers. The increasing values of these two types may indicate the increased incidence of fire in the Park.

In summary, the site depicts the development of monte negro hygrophytic shrub vegetation after the abandonment of agriculture in the 1890's. The Pinus populations were logged and subsequently replanted. The site shows greater evidence of stability at time goes by, with increasing Phillyrea, and evidence that fires are becoming more frequent also occurs.

CHAPTER 6

VEGETATION CHANGES IN THE GUADALQUIVIR BASIN OVER THE LAST 13,000 YEARS

The earliest records of vegetation from the Doñana area during the Flandrian, derive from the interbedded sands and peats at El Asperillo (Chapter 3). (Reference to Table 23 will give approximate time-vegetation events). The bands have been dated to about 13,000 BP and represent dune/dune slack successional vegetation, analogous to the processes seen nowadays in the Doñana National Park. (Torres Martinez et al 1975). A noticeable difference between the two systems is the greater evidence of stability for the fossil Asperillo dune slacks. Before the ultimate destruction of the slack by the next dune front, the vegetation reaches a more advanced stage in the successional sequence, i.e. Juniperus invasion and lagoonal conditions with Typha latifolia and possibly Salix present, both of which nowadays are restricted to more stable conditions. Apart from the purely local indication of the environment at this time, the site also reveals evidence about the regional forests of the area, for the bands have inputs of regional pollen in excess of those into comparable modern day sites (i.e. Alnus, Corylus and Betula). These suggest the existence of a cool moist forest nearer to the Doñana area that at present, as such forests are found nowadays only in deep gorges in the Sierra Morena, 200km away to the north, then this forest must have subsequently contracted to its present range. The presence of a continued Ephedra input can confirm this view, for it is known that most of upland Spain at this time was experiencing steppe

like conditions (Florschutz et al 1971). Thus all the forest belts would have been at lower altitudes and this can explain the existence of the cool moist forest on the Guadalquivir plain at this time.

A gap now occurs in the pollen record until the initiation of the deposits in Laguna de las Madres (approx. 4500 b.p.). Therefore little can be surmised about the vegetational change during this intervening period, however, the existence of iron bands above the peat bands at Asperillo may indicate even more moister times (though not necessarily cool).

The pollen record from Laguna de las Madres reveals the existence of a Mediterranean type of vegetation, but one that is already heavily disturbed (although the initial disturbance may have had a tectonic origin, i.e. active mobile sand dunes). Because of the lateness of peat initiations, the vegetation of the area would undoubtedly already have felt the impact of man and thus the initial state of the vegetation before this impact cannot be elucidated. The core reveals several changes in the forest vegetation of the area. Initially before 4500 b.p., the regional forest consisted of Quercus and Pinus, Quercus occupying the wetter soils and Pinus the unstable drier soils. These forests then almost disappeared during a period of high soil disturbance (of high Chenopodiaceae and Liguliflorae), the cause of the disturbance probably being related to the activities of the mobile sand dunes, which at this time blocked off the outflow of the Laguna. However, the forests recovered to something approaching their former condition by 4500 b.p. It was during the following period

that evidence for extensive viticulture occurs which lasted until about 2220 b.p. where cultivation was abruptly terminated, and is correlated with Quercus which reaches its peak after this abandonment of cultivation. The Pinus forest during this intervening period suffered very extensively, first the values from Pinus became very erratic only finally to disappear, at which point an expansion in Juniperus took place. Although stabilisation of soils may have caused the switch from Pinus to Juniperus, human interference in the vegetation has become very evident. After Quercus reaches its maximum value about 1700 b.p., they then fall steeply away as another phase of forest disturbance gets under way, with large expansions in Pinus and Juniperus, which may be explained in terms of falling water tables, however, pastizal indicators are very high and the evidence suggests an extensive population of Pinus occurring around the Laguna at this time. The pastizal indicators appear to have originated from the Pinus forest and the indications are that the Pinus had been introduced and planted, perhaps on the soil cleared of monte negro hygrophytic shrub and forest. However, this does not explain the Juniperus increase which may indeed be related to falling water tables. The forests after this phase of disturbance vary in their behaviour; the Quercus forest appears to maintain itself in a stable state, whilst both the Pinus and Juniperus values fall very heavily probably due to extensive logging of both populations in the 19th and 20th centuries.

Running concurrently with the last portion of the core from Laguna de las Madres (i.e. from 1700 onwards) exists a core

from within the Doñana National Park. This core reveals the existence of a scattered Pinus population in typical monte negro type shrub vegetation, as is found nowadays. The Pinus population subsequently declines (probably due to logging) until it disappears. After this disappearance comes the first indications of a Quercus forest, the values of which finally records high values and represents the last portion of Quercus suber forest in the region. The core cannot relate the processes occurring in the rest of the vegetation, once the canopy has closed, due to pollen flow problems in monte negro hygrophytic forest vegetation. However, before the Quercus increase, the indications are that the populations of Q. suber in the Park were very similar to that of todays. No indications of full forest cover are recovered, nor, because of the position of the core, can the history of the area that supported Q. suber be fully elucidated.

TABLE 23

FOREST CHANGES IN THE GUADALQUIVIR BASIN

OVER THE LAST 13,000 YEARS

YEARS B.P.	FOREST CONDITIONS
13,000	Cool moist forest of *Betula*/*Corylus* present
Hiatus	
Pre 4,550	*Quercus*/*Pinus* forest - heavy disturbance present - forest eventually recovers
4,550-2,220	Viticulture, *Pinus* erratic and finally disappears- *Quercus* increases. *Pinus* replaced by *Juniperus*.
2,220	End of viticulture
2,220-1,700 approx.	*Quercus* recovers to maximum - *Juniperus* falls
1,700-present	1) *Quercus* falls, *Juniperus* and *Pinus* forests increase only to subsequently fall due to logging.
Encinillas Altas 210-present	1) Scattered *Pinus* in monte negro 2) *Pinus* removed and monte negro replaced by *Quercus*.

BIBLIOGRAPHY

Aario, L. 1940. Waldgrenzen und subrezente Pollenspektren in Petsamo, Lapland. Ann. Acad. Scient. Finn. A,54.

Aario, L. 1944. Uber die pollenanalytischen Methoden zur Untersuchung von Waldgrenzen. Geol. Foren. Stock. Forh. 66. 337-354.

Adam, D.S. and Mehringer, J. 1975. Modern pollen surface samples - and analysis of subsamples. Journal of U.S. Survey 3 (6) 733-36.

Allier, C., Gonzalez Bernaldez, F., Ramirez Diaz, L. 1974. Reserva Biologica de Donana - Ecologica Map. Estacion Biologica de Donana CSIC, Sevilla.

Andersen, S.T. 1970. The relative pollen productivity and representation of N. European trees, and correction for tree pollen spectra. Danm. geol. Unders. Ser.II. 96. 99pp.

Beaulieu, J. 1977. Contribution Pollen analytique a L'histoire Tardiglaciare et Holocene de la Vegetation des Alpes Meridionales Francaises. Thesis at Universite d'Aix - Marseille 3.

Beug, H-J. 1957. Unterschungen zur spatglazialen und fruhpost-glazialen Floren - und Vegetation-geshichte einiger Mittelgebirge. Flora 145 167-211.

Beug, H-J. 1961. Leitfaden der Pollen bestimmung. Stuttgart.

Beug, H-J. 1967. On the forest history of the Dalmation Coast. Reviews of Palaeobotany and Palaeoecology 2 271-79.

Birks, H.J.B. 1973. Past and present vegetation of the Isle of Skye: A Palaeoecological study. C.U.P.

Bobek, H. 1959. Features and formation of the Great Kavir and Masileh Arid Zone Centre. University of Tehran. Pub. No.2 1-63.

Bottema, S. 1974. The Late Quaternary Vegetation history of Northwestern Greece. Unpublished PhD. thesis Groningen.

Bottema, S. and Barkoudah, Y. 1979. Modern pollen precipitation in Syria and Lebanon and its relation to Vegetation. Pollen et Spores. 21. 427-480.

BIBLIOGRAPHY

Caratini, C. and Viguier, C. 1973. Etude palynologique et sedimentologique des sables hologene de la falaise littoral d'el Asperillo. Estudios Geologicos, 29, 325-328.

Caseldine, C.J. 1981. Surface pollen studies across Bankhead Moss, Fife, Scotland. Journ.Biogeog., 8, 7-26.

Chapman, V.J. 1976. Coastal vegetation. Pergamon, Oxford & London.

Clarke, G.C. 1977. The Northwest European pollen flora 10- Boraginaceae. Reviews of Palaeobotany and palyonology. 24, 59-101.

Colinvaux, P. 1964. The Environment of the Bering Land Bridge. Ecological Monographs, 34, 297-329.

Coombe, D.E., Douse, A.F.G., Preston, C.D. 1981. The vegetation of Ringmere in August, 1974. Proceedings of Norfolk Naturalist Society, 25, 206-317.

Davies, J.L. 1972. Geographical Variation in Coastal Development. Oliver and Boyd, Edinburgh.

Eckholm, 1976. Losing Ground. W.W. Norton, New York..

Erdtman, G. 1960. The Acetolysis Method. Svensk. bot. Tidskr, 54, 561-64.

Evenari, M., Sharian, L. and Tadmor, N. 1971. The Negev: the challenge of a desert. 345pp. Harvard, Cambridge, Mass.

Faegri, K. and Iversen, J. 1964. A textbook of pollen analysis. Munksgaard, Copenhagen. 2nd ed, 237pp.

Figueroa, E. 1976. Ecologia del Pinus pinea en el Parque Nacional de Doñana. Tesina de Licenciation, Universidad de Sevilla.

Florschutz, F., Menendez Amor, J. and Wijmstra, T.A. 1971. Palynology of a thick Quarternary succession in S. Spain. Palaeogeography, Palaeoclimatology, Palaeoecology. 10, 233-264.

Freitag, H. 1982. (In Press) In:- Desertification in Social Perspective. Ed. by B. Spooner and H.F. Mann. Academic Press.

BIBLIOGRAPHY

Fredskild. 1967. Palaeobotanical investigations at Sermermuit Jakobshaven, W. Greenland. Meddr. Gronland. 178, 54p.

Gabriel, A. 1957. Zur Oberflachengestaltung der Pfannen in den Trockenraumen Zentralpersiens. Mitteil. Geogr. Gesellsch., Wien.

Garcia Novo, F., Ramirez Diaz, L., Torres Martinez, A. 1975. El Sistema de dunas de Doñana. Naturalia Hispanica No. 5. ICONA Ministerio de Agricultura, Madrid.

Garcia Novo, F. 1977. Effects of Fire on the Vegetation of the Doñana National Park (Spain), Symposium on the Environment. Consequences of Fire and Fuel Management in Mediterranean Ecosystems. U.S.D.A. Technical Report WD-3, pp.318-25.

Garvia Novo, F. 1979. The Ecology and Vegetation of the dunes in Doñana National Park (South West Spain). In Ecological Processes in Coastal Environments. Ed. Jeffries, R.L. and Davy, A.J. pp.571-94.

Gonzalez Bernaldez, F., Garcia Novo, F., Ramirez Diaz, L. 1975. Analyse factorielle de la vegetation des dunes de la Reserva Biologique de Doñana (Espagne). I. Analyse numerique des dunes floristiques. Israeli Journal of Botany, 24, 106-117.

Gonzalez Bernaldez, F., Garcia Novo, F., Ramirez Diaz, L. 1975. Analyse factorielle de la vegetation des dunes de la Reserva Biologique de Doñana (Espagne). II. Analyse d'un gradient du milieu. Etude speciale du probleme de la non-linearite. Israeli Journal of Botany, 24, 173-182.

Granados Corona, M. 1980. Historia de Doñana. Departamento de Ecologia, Facultad de Biologia, Universidad de Sevilla.

Grichok. 1950. The vegetation pf the Russian plains in early and middle Quarternary times. Tr. Inst. Gegr. Navk. S.S.S.R. 46, 5-202 (In Russian).

Harrant, H. and Jarry, D. 1967. Guide du Naturaliste dans le Midi de la France. Delanchaux et Niestle, Neuchatet.

Havinga, A.J. 1959. Palynology and Pollen Preservation. Reviews of Palaeobotany and Palyonology, 2, 81-98.

Hedin, S. 1910. Overland to India. 2 vol. London.

Hevly, 1968. Modern pollen rain in N. Arizona. Journal of Arizona Academy of Science. 5, 116-127.

Horne, L. 1980. Village Morphology. "Expedition" - University Museum Magazine of Archaeology and Anthropology, University of Pennsylvania. Vol.22, 11-17.

I.G.M.E. (Instituto Geologico y Minero de Espana). 1972. Mapa Geologico de Espana 1:200,000. 80-81. Ayamonte-Huelva. Madrid.

I.G.M.E. 1975. Mapa Geologico de Espana. Hoja 1.017. 10-42. 1:50,000. Madrid.

I.G.M.E. 1976. Mapa Geologico de Espana. Hoja 1.000. 10-41. 1:50,000. Madrid.

Iversen, J. 1952. Origin of the flora of W. Greenland in the light of pollen analysis. Oikos 4, 85-103.

Jowsey, P.C. 1966. An improved peat sampler. New Phytologist, 65, 245-48.

Krinsley, D.B. 1970. A Geomorphological and Palaeoclimatological study of the playas of Iran. Final Scientific Report no. PRO CP 70-800. 2 vols. ppd. for Air Force Cambridge Research Labs., Mass.

Lichti-Federovich, S. and Ritchie, J.C. 1968. Recent pollen assemblages from the Western Interior of Canada. Review of Palaeobotany and Palyonology, 7, 297-344.

Machin, J. 1971. Plant microfossils from Tertiary deposits of the Isle of Wight, New Phytologist, 70, 851-72.

Maher, L.J. 1964. Ephedra pollen in the sediments of the Great Lakes region. Ecology 45, 391-95.

Martin, H.A. 1973. Palyonology and historical ecology of some cave excavations in the Australian Nullabar. Australian Journal of Botany, 21, 283-316.

McAndrew, J. and Wright, H.E. 1969. Modern pollen rain across the Wyoming Basin and the Northern Great Plains (USA). Reviews of Palaeobotany and Palyonology, 9, 17-43.

BIBLIOGRAPHY

Menedez Amor, J. and Florschutz, F. 1964. Resultados del analisis paleobotanico de una capa de turba en las cercanias Huelva. Estudios Geologicos, 20, 183-86.

Menenteau, L. 1981. Aqui estaba Tartessus. Gaceta Illustrada, No.1278, 28-44. Madrid.

Merino, J., Garcis Novo, F., Sanchez Diaz, M. 1976. Annual fluctuation of water potential in the xerophytic shrubs of the Donana Biological Reserve (Spain). Oecol. Plant. 11, 1-11.

Moore, P.D. and Webb, J. 1978. An Illustrated Guide to Pollen Analysis. Hodder and Stoughton, London.

Mountfort, G. 1968. Portrait of a Wilderness. David and Charles, Newton Abbot.

Pou, A. 1976. Implicaciones paleoclimaticas de la sistema dunares de Donana. V. Reunionde Climatologia Agricola. Universidad de Santiago de Compostela.

Prentice, I.C. 1980. Modern Pollen Spectra from lake sediments in Finland and Finnmark, North Norway. Boreas, 7, 131-153.

Quezel, P. 1977. Forests of the Mediterranean basin - in Mediterranean forest and maquis: ecology, conservation and management. MAB Technical notes. U.N.E.S.C.O. p.9-32. France.

Ranwell, D.S. 1972. Ecology of Salt Marshes and Sand Dunes. Chapman and Hall, London.

Rechinger, K.H. 1963- Flora Iranica. Graz.

Rechinger, K.H. 1977. Plants of the Touran protected area, Iran - Iranian Journal of Botany 1 (1) 23-56.

Reille, M. 1975. Contribution pollen analytique a l'histoire tardiglaciare et Holocene de la Vegetation de la Montagne Corse. Thesis at Universite d'Aix - Marseille 3.

Ritchie, J.C. 1974. Modern Pollen Assemblage near the Arctic Tree Line, Mackenzie Delta Region. N.W. Territories. Canadian Journal of Botany, 52, 381-396.

BIBLIOGRAPHY

Sabeti, H. 1976. Forest, Trees and Shrubs of Iran. Ministry of Agriculture and Natural Resources, Tehran. (In Persian).

Schoenwetter. 1973. Archaeological pollen analysis of sediment samples from Asto village settlements. In "Les Etablissements Asto a l'Epoque Prehistorique". Travaux de l'Institut Francais d'etudes Andines. 15, 101-111. Lima, Peru.

Schoenwetter. 1974. Pollen records of Guila Naquitz cave. American Antiquity, 39, 292-303.

Schoenwetter and Doerschlag. 1971. Surficial pollen records from Central Arizona. 1. Sonoran desert scrub. Journal of the Arizona Academy of Science, 6, 216-221.

Schulz. 1980. Present pollen rain in the Central Sahara. Proceedings of 5th Int. Palynological Conf. Cambridge.

Seddon, B. 1967. Lacustrine Environment and Macrophytic Vegetation, 205-215. In "Quarternary Palaeoecology". Ed. by Cushing and Wright. Y.U.P.

Singh, G., Chopra, S.K., Singh, A.B. 1973. Pollen rain from the vegetation of North West India. New Phytologist, 72, 191-206.

Spooner, B.S. 1980. Introduction - Expedition (University Museum Magazine of Archaeology and Anthropology, University of Pennsylvania. 22, 4-10.

Steeves, M.W. and Barghorn, E.S. 1959. The pollen of Ephedra. The Journal of Arnold Arboreum, 40, 221-55.

Tauber, H. 1965. Differential pollen dispersion and the interpretation of pollen diagrams. Danmarks Geol. Undersogelse, 11, 1-69.

Tauber, H. 1967. Investigations of the mode of pollen transfer in forested areas. Review of Palaeobotany and Palyonology, 3, 277-286.

Teresmae. 1967. Recent pollen deposition in the North Eastern district of Mackenzie. (N.W. Territories, Canada). Palaeogeography, Palaeoclimatology, Palaeoecology. 3, 17-27.

BIBLIOGRAPHY

Tinsley, H. and Smith, R.T. 1974. Surface pollen studies across a woodland/heath, transition and their application to the interpretation of pollen digs.

Torres Martinez, A., Allier, C., Ramirez Diaz, L., Garcia Novo, F. Sistema de Dunas in 'Doñana prospeccion inventario de ecosistema' pp.195-224. ICONA 18, Ministerio de Agricultura, Madrid.

Turner, C. 1970. The Middle Pleistocene Deposits at Marks Tey, Essex. Phil. Trans. Royal Soc. B 257, 373-440.

Turner, J. 1964.a.The anthropogenic factor in vegetational history. 1. Tregaron and Whixall Mosses. New Phytologist, 63, 73-90.

Turner, J. 1964.b. Surface Sample analyses from Ayrshire, Scotland. Pollen Spores, 6, 583-92.

Tutin, T. et al. 1964-1980. Flora Europea Vol.1-5.

Tyldesley, J.B. 1973. Long range transmission of tree pollen to Shetland. 1. Sampling and Trajectories. New Phytologist, 72, 175-181.

Van Zeist, W., Timmers,R.W., Bottema, S. 1968. Studies of modern and Holocene pollen precipitation in S.E. Turkey. Palaeohistoria, 14, 19-39.

Van Zeist, W., Woldring, H.,and Stapert, D. 1975. Late Quarternary vegetation and climate of S.W. Turkey. Palaeohistoria, 17, 55-143.

Van Zeist, W. and Bottema, S. 1977. Palynological investigations in W. Iran. Palaeohistoria, 19, 19-95.

Vanney, J.R. and Menenteau, L. 1979. Types de Reliefs Littoraux et Dunaires en Basse Andalousie (de la Ria de Huelva a l'embochure du Guadalquivir). Melanges de la Casa de Velazquez. Tome XV. 4-51.

Vinje, J.M. and Vinje, M.M. 1955. Preliminary aerial survey of microbiota in the vicinity of Davenport, Iowa. American Midland Naturalist, 54, 418-432.

Way. 1957. A geography of Portugal and Spain. Methuen and Dutton.

BIBLIOGRAPHY

Welten, M. 1957. Uber das glaziale und spatglazial Vorkommen von Ephedra an nordwestlichen Alpenrand. Berichte der Schweizen Botanischen Gesellschaft, 67, 33-54.

Wendelbo, P. 1976. An annotated check list of the ferns of Iran. Iranian Journal of Botany 1. (1) 11-17.

Winstanley. 1973. Past and present rainfall patterns in the Sahara. Nature, 245, 190-194.

Wright, H.E., McAndrews, J.H., Van Zeist, W. 1967. Modern pollen rain in W. Iran, and its relation to plant geography and Quaternary vegetational history. Journal of Ecology, 55, 415-43.

Young, S.B. and Schofield, E.K. 1973. Pollen evidence for late Quaternary climate changes in Kerguellen Islands. Nature, 245, 311-312.

Zohary, M. 1973. Geobotanical foundations of the Middle East. Stuttgart, Gustav Fischer Verlag.

ADDENDA:

Birks, H.J.B. 1973. Modern pollen studies in some Arctic and Alpine environments. IN Quaternary Plant Ecology. B.E.S. Symposium, ed. H.J.B. Birks and R.G. West. Blackwell, London.

Ritchie, J.C. and Lichti-Federovich, S. 1967. Pollen dispersal phenomena in Arctic - sub-Arctic Canada. Reviews of Palaeobotany and Palynology, 3. 255-266.

APPENDIX A

Comments on pollen mophology

and

keys to certain groups

Pinaceae

An unpublished key of Dr. P.D. Moore was used to assign saccate grains to particular pollen types.

Key to saccate grains (after P.D. Moore)

1a Sacci not constricted at point of attachment to the body of the grain. Area of sac attachment large in comparison to the distance between sacs.----------2

1b Sacci constricted at the point of attachment to the body of the grain. Area of sac attachment small in comparison to distance between sacs.----------3

2a Distal portion of the grain body(area between sacs) finely rugulate. Body wall of irregular thickness.....*Cedrus*

2b Distal portion of the grain body with dense, small verrucae(Ph). Body wall of even thickness.....*Picea*

3a Body of grain in size range 40-70 µm----------4

3b Body of grain in size range 75-160 µm----------*Abies*

4a Conspicuous verrucae on distal portion of the grain body (between the sacs use Ph).....*Pinus* subgenus haploxylon (inc. *P.strobus*, *P.cembra*, *P.siberica* *P.wallichiana*, *P.peuce*, *P.aristata*)

4b No verrucae on distal portion of the grain body....*Pinus* subgenus *Pinus*

Abies pinsapo the only Spanish Abies is normally >120 µm in body diameter. It was not possible on size distinctions to differentiate the three *Pinus* species, which were likely candidates for the pollen input into the Spanish sites.

Ephedraceae

Accounts of the pollen morphology of the family have been published by Steeves and Barghorn (1959) and Welten (1957). Within the present European taxa, two pollen types can be distinguished(Beug 1957,1961)

Ephedra fragilis type
Furrows (not true colpi) are present which are unbranched. Furrow number is usually greater than 9.

Ephedra distachya type
4-7 furrows present, which are branched and the lateral branches extend up onto the meridional ridges.
Includes:- E.distacya, E.helvetica, E.major, E.intermedia

Fagaceae

An attempt was made to try and separate the evergreen oaks from the summer deciduous ones, but while there appeared to be distinctions between the two, a large range of variation was found on all type slides, that cast doubt on a clear cut separation. Quercus suber, which was the main species thought to be responsible for the pollen input into the Spanish sites, was in any case found to be very similar to the deciduous oak types (A feature recognised by Beug(1965)

Urticaceae

The Urticaceae can be divided up into five main pollen

morphological types, these are :-

Urtica dubia type

Polypantoporate grain, < 30μm, scabrae evenly scattered and pori do not possess an annulus and are slightly sunken.

Urtica dioica type

Grains <20μm, trizonoporate (sometimes tetrazonoporate), pori possess an annulus, sculpturing is irregular scabrae.

Urtica urens type

Grain less than 20μm, trizonoporate, pori possess an annulus, scabrae present which are regularly scattered.

Urtica pilulifera type

Polypantoporate grains (6-7 pores), grain>35μm. Pori annulate and scabrae are regular and evenly scattered, sometimes verrucae are apparent.

Parietaria type

Trizonoporate grains, which are <20μm, scabrae are irregular and pori are not annulate.

Key to the Urticaceae

1a Grains trizonoporate----------2

1b Grains tetrazonoporate or polypantoporate----------4

2a Porus not thickened to an annulus----------Parietaria type

2b Porus thickened into an annulus----------3

3a Scabrae evenly scattered over the grain-----Urtica urens type

3b Scabrae coarse and irregularly scattered over the grain ----------Urtica dioica type

4a Grain large >35μm, pori not sunken and is annulate----------Urtica pilulifera type

4b Grain small <30μm, pori sunken and no annulus to the pore----------Urtica dubia type

Santalaceae

Thesium humifusum

Syncolpate grain, which is composed of three colpi which fuse at one pole only, and form a trilete mark, sculpturing is reticulate which is heterobrochate with the lumina getting markedly smaller towards the colpus edge, from which the reticulum is absent forming a margo which is psilate/perforate.

Osyris alba

Trizonocolporate grains, microreticulate with costae colpi.

Rafflesiaceae

Cytinus ruber

Grains in irregular tetrads, which are small <20µm and which are psilate.

Balanophoraceae

Cynomorium coccimeum

Trizonocolpate reticulate grains, apocolpium very small, lumina of reticulum decrease to the colpus edge leaving a distinct margo.

Polygonaceae

Atraphaxis

Trizonocolporate grains, colpi long and costate,pore indistinct, sculpturing striate, tectum is tectate perforate.

Calligonum type

Trizonocolporate grains, with long costae colpi, with a distinct pore that is meridionally elongated. Surface sculpturing is psilate-tectate perforate.

Includes Pteropyrum

Rheum type

Trizonocolporate grains, with long costae colpi with a distinct pore that is equatorially elongated, wall 1.5um thick and sculpturing is psilate-tectate perforate.

Molluginaceae

Glinus lotoides

Trizonocolpate grains with a small apocolpium, columellae distinct and coarse, grain is probably indistinguishable from the Scrophulariaceae

Caryophyllaceae

Illecebrum

Polypantoporate grains (5-6 pores), <20µm, surface sculpturing is psilate.

Loeflingia type

Trizonocolpate grains, <25µm, columellae distinct and grain is as long as broad.

Ranunculaceae

Delphinium type

Trizonocolpate grains, with long colpi, walls thickest at the poles and the wall is smooth.

Ceratocephalus type

Trizonocolpate grains, with crack like colpi which almost fuse in the apocolpium. Large wall elements surrounded by a ring from which the columellae are absent.

Papaveraceae

Rupicapnos

This grain will key out with Fumaria in the key of Moore and Webb (1978).

Sarcocapnos

Tetrazonocolpate grain, with all four colpi fusing at one pole. Columellae longest at the corners of the grain and gives a triangular appearance. Sculpturing is mainly tectate-perforate. At the poles the columellae become very distinct.

Leguminosae

Onobrychis type

Trizonocolpate grains which are reticulate, with the lumina getting smaller towards the colpus edge.

Robinia pseudoacacia

Trizonocolporate grains, grain as long as broad with scabrate/verrucate sculpturing.

Lotus type

Trizonocolporate grains, <20 µm, grain longer than broad with psilate sculpturing, colpi narrow and crack like, costae present.

Includes:- Tetragonobolus, L. corniculatus, L. tenuis, L. pedunculatus, L. uliginosus, L. creticus.

Coronilla type

Trizonocolporate grains, <20 µm, grain longer than broad, with striate sculpturing which is visible only at X1000.

Medicago sativa type

Trizonocolporate grains, which are longer than broad with scabrate/verrucate sculpturing (sometimes rugulate). Endoporus not well developed and pore is a crack in the colpus.

Includes :- Trigonella, M. polymorpha, M. sativa, M. falcata.

Vicia cracca type

Trizonocolporate grain with a prominent endoporus which is nexinously thickened. Sculpturing is scabrate/verrucate.

Includes :- V. sepium, V. cracca, Lathyrus montanum, Dorycnicum and Glycyrhiza

Ornithopus sativus type

Trizonocolporate grains with a distinct endoporus that is often meridionally contracted. Sculpturing is scabrate/verrucate in the mesocolpium, psilate in the apocolpium.

Grain small < 30 μm

Inc.:- O. perpusillus, O. compressus

Anthyllis vulneraria

As for Ornithopus sativus but scabrae/verrucae are present in the apocolpium and the grain is large >35 μm.

Melilotus type

Trizonocolporate suprareticulate grain that is longer than broad with more than fifteen lumina across the mesocolpium, the reticulum is well developed in both the meso and apocolpium. Some of the lumina in the middle of the mesocolpium are smaller than those at the colpus edge and an endoporus is obvious.

Includes:- Ononis repens, Lens culinaris, Hedysarum, M. altissima, M. alticus

Adenocarpus type

As for Melilotus but reticulum gets smaller to the colpus edge and the costae are interuppted for more than half their length.

Includes :- Galega, Agyrolobium and Lupinus

Cercis type

As for Melilotus but reticulum is constant and the colpi are not interrupted for more than half their length.

Includes :- Ceratonia and Cercis.

Lathyrus type

Trizonocolporate grains with a suprareticulum that is well developed in the apocolpium and the costae are well developed reaching a thickness of 3X that of the rest of the exine, porus is also well developed.

Includes :- L. japonica, L. nissiola, L. latifolius, L. maritimus, L. boisseri.

Astragalus type

As for Lathyrus but costae are less than 3X the thickness of the rest of the exine and the porus is not well developed.

Includes :- A. danicus, A. hispanicus, A. glycyphytes, Trifolium fragiferum, T. dubium, T. repens, T. baudium, Oxytropis, Colutea, Medicago arabica

Phaseolus vulgaris

Trizonocolporate suprareticulate grains with less than 15 lumina across the mesocolpium, colpi are short and are less than half the length of the grain, pores are prominent.

Pisum sativum

Trizonocolporate suprareticulate grains with less than 5 lumina across the mesocolpium and the grain is large > 45 µm

Ononis baetica type

Trizonocolporate suprareticulate grains with less than 15 lumina acroos the mesocolpium, grain < 45 µm, pore is ill defined and reticulum is distinct in the apocolpium and mesocolpium, columellae are fine to indistinct.

Includes:- Melilotus officinalis, M. indica, M.alba, and some grains of Lygos monosperma

Trifolium arvense type

As for O. baetica but reticulum is absent from the apocolpium and the columellae are distinct.

Includes :- T. arvense, T. subterranum, T. striatum, T. squarrosum, T. montanum, T. incarnatum.

Vicia sylvatica type

As for O. baetica but the porus is well defined and thickened nexinously and the columellae are fine-indistinct.

Includes :- V. angustifolia, V. tetraspermum, V. orobus, V. hirsutum, Lathyrus odoratus, L. pratensis, Biserrula.

Scorpiurus

As for O. baetica except that the pore is prominent and the muri wind.

Trifolium micranthum type

As for O. baetica but porus is prominent and is meridionally contacted and the reticulum is not well developed in the apocolpium.

Includes :- T. micranthum and T. campestre.

Psoralea bituminosa

Grain as long as broad, trizonocolporate suprareticulate, muri wind and there are only 3-4 lumina across the mesocolpium, colpi are short approximately half the length of the grain.

Genista type

Grain as long as broad, trizonocolporate suprareticulate grains with an indistinct pore.

Includes :- Genista, Ulex, Stauracanthus, Lotononis, Cytisus, Spartium, Echinospartium, Chamaespartium, Teline, Chronanthus, Chamaecytisus, Calicotome.

Key to the Leguminosae

1a Porus absent and costae absent----------*Onobrychis* type

1b Porus present as a rupture in the colpus or a neat pore
----------2

2a Grain psilate/scabrate/verrucate/striate but never suprareticulate.----------3

2b Grain suprareticulate----------9

3a Grain as long as broad----------*Robinia pseudoacacia*

3b Grain longer than broad----------4

4a Grain < 20 µm----------5

4b Grain > 20 µm ----------6

5a Grain psilate---------- *Lotus* type

5b Grain striate---------- *Coronilla* type

6a Endoporus not well developed and pore is a crack in the colpus, sculpturing scabrate/verrucate---- *Medicago sativa* type

6b Endoporus well developed and circular/elongate never rectangular----------7

7a Endoporus prominent and thickened nexinously
---------- *Vicia cracca* type

7b Endoporus not thickened and often meridionally contacted----------8

8a Grain has distinct scabrae/verrucae in the mesocolpium only, grain < 30 µm---------- *Ornithopus sativus* type

8b Grain has distinct s/v in both the apo and mesocolpium, grain > 35 µm---------- *Anthyllis vulneraria*

9a Grain longer than broad----------10

9b Grain as long as broad----------21

10a More than 15 lumina across the mesocolpium----------11

10b Less than 15 lumina across the mesocolpium----------15

11a Reticulum well developed in both the apo and mes-
colpium----------12

11b Reticulum well developed in the mesocolpium only and
columellae often distinct----------14

12a Some of the lumina in the middle of the mesocolpium
are smaller than those at the colpus edge and an
endoporus is obvious---------- *Melilotus* type

12b Size of the lumina either decrease to the colpus edge
or is constant and the endoporus is a crack in the
colpus----------13

13a Reticulum gets smaller to the colpus edge and the costae
are interuppted for more than half the length of
the grain---------- *Adenocarpus* type

13b Reticulum is of a constant size and the costae are not
interrupted for more than half their length.
---------- *Cercis* type

14a Costae well developed, > 3X as thick as rest of the
exine, Porus well developed----------*Lathyrus* type

14b Costae < 3X the thickness of the rest of the exine.
Porus not well developed----------*Astragalus* type

15a Colpi < half length of the grain-----*Phaseolus vulgaris*

15b Colpi at least half the length of the grain--------16

16a Grain > 45 μm and < 5 lumina across the mesocolpium
---------- *Pisum sativum*

16b Grain < 45 μm and > 5 lumina across the mesocolpium-17

17a Porus ill defined and ± costae----------18

17b Porus distinct and is circular or meridionally
contracted----------19

18a Reticulum well developed in the apocolpium, columellae indistinct---------- Ononis baetica type

18b Reticulum absent from the apocolpium and the columellae are distinct---Trifolium arvense type

19a Porus circular and thickened nexinously, columellae fine-indistinct---------- Vicia sylvatica type

19b Porus not thickened and columellae are distinct-----20

20a Porus circular and muri wind----------Scorpiurus

20b Porus meridionally contracted, muri do not wind, reticulum not well developed in the apocolpium. ----------Trifolium micranthum type

21a Porus well defined, colpi short < half the length of the grain. 3-4 lumina across the mesocolpium and muri wind---------- Psoralea bituminosa

21b Porus indistinct and colpus only slightly constricted. ---------- Genista type

i) Some grains of Medicago littoralis will key out here but can be separated on the presence of costae.

ii) Lygos may be differentiated on less than 15 lumina across the mesocolpium.

iii) Genista tinctoria may be differentiated on its large size which is > 40 µm.

Geraniaceae

Erodium

Trizonocolpate grain > 40 µm. Columellae are large and distinct. Grain can be distinguished from Geranium by the striae which run across the coarse columellae.

Zygophyllaceae

Zygophyllum

Trizonocolporate microreticulate grains, the grain is longer than broad.

Peganum

Trizonocolporate microreticulate grains, the grain is as long as broad.

Tribulus

Polypantoporate grains, pori sunken amongst the large prominent columellae.

Linaceae

Linum anglicum

Trizonoporate grains, baculate which are of two different sizes

Linum catharticum type

Trizonocolpate grains, baculate which are all the same width or no more than 2X the width. Grain >20 μm and the number of baculae across the mesocolpium is > 20

Includes L. setaceum, L suffruticosum, L. tenuifolium

Radiola

Trizonocolpate grain, baculate and grain is < 20 μm and no of baculae across the mesocolpium is < 10.

Linum narbonense

Trizonocolpate grains, baculate, grain is large > 95 μm, baculae of different widths at least 2X the difference between the large and small ones.

Linum bienne

As for Linum narbonense but grain are all < 95 μm.

Includes L. campanulatum, L. maritimum, L. perenne, L. strictum,

L. tenue, *L. viscosum*.

Key to the Linaceae

1a Grain trizonoporate----------*Linum anglicum*

1b Grain trizonocolpate----------2

2a Baculae all same width or no more than 2X the difference between the sizes----------3

2b Baculae of different widths at least 3X the difference between the large and small----------4

3a Grain small < 20 μm, < 10 baculae across the mesocolpium ----------*Radiola*

3b Grain > 20 μm and > 20 baculae across the mesocolpium ----------*Linum catharticum* type

4a Grain > 95 μm----------*Linum narbonense*

4b Grain < 95 μm----------*Linum bienne* type

Rutaceae

Citrus sp.

Tetrazonocolporate grains, with a coarse reticulate sculpturing, columellae are distinct.

Simaroubaceae

Ailanthus altissima

Trizonocolporate grain with the porus elongated equatorially, columellae distinct with striate sculpturing to reticulate, costae colpi present.

Meliaceae

Melia azedarach

Trizonocolporate grains, with a verrucate/scabrate sculpturing.

Coriariaceae

Coriaria myrtifolia

Tetrazonoporate grains, slightly elongate, with verrucate/ scabrate sculpturing.

Anacardiaceae

Pistacia

Two type may be distinguished within this genus:-

i) Pistacia khinjuk type

Tetrazonoporate grain with indistinct pores and a reticulum.

ii) Pistacia lentiscus type

Polypantoporate grain with a reticulum (10-12 pores) pores are more distinct than in i)

Includes P. terebinthus

Rhus

Trizonocolporate grains , reticulate , sitting in a striate pattern which runs in all directions.

Schinus

Trizonocolporate grains, reticulate, with the reticulum sitting in a heavy striate pettern and which run from pole to pole.

Thymeleaceae

Thymelea hirsuta

Inaperturate grains, with large prominent columellae forming a reticulum as they fuse at the top, small echinae sit on the reticulum.

Daphne

Polypantoporate grains (10-15 pores), pores are diffuse and punctured through the tectum which consists of large

prominent columellae. D, gnidium may be separated from D. laureola on the basis of size (D. laureola is larger) and the more echinate columellae of D. laureola

Cistaceae

Helianthemum

Trizonocolporate grains, columellae small < 0.5 µm which do not form a definite reticulum but join at the ends into striae which run from pole to pole.

Includes H. oelandicum , H. chamaecistus, H. croceum

Halimium type

Trizonocolporate grains, with the large prominent columellae > 2 µm thick sitting in a reticulate pattern with the walls of the lumina further being arranged into pole to pole striae.

Cistus ladanifer type

Trizonocolporate grains with a reticulum, lumina are large at least some greater than 4 µm, the lumina also decrease to the colpus edge.

Includes:- C. populifolius, C. monspeliensis, C. laurifolius.

Cistus salvifolius type

Trizonocolporate grains, reticulate, wall of the lumina are not arranged into pole to pole striae. If striae are present then they are very short and run in all directions. Lumina are small < 1 µm and columellae < 1.5 µm.

Includes:- C. salvifolius, C. varius, C. psilosepalus, C. crispus, C. clusii, C. incarnartum, C. villosus, C. albidus, Tuberaria guttata, T. bupleurifolia

Key to the Cistaceae

1a Columellae large > 1 μm and unite into a reticulum---2

1b Columellae small < 1 μm, which do not unite into a reticulum but into distinct pole to pole striae ---------- Helianthemum

2a Lumina large(at least some > 4 μm) and lumina decrease in size to the colpus edge----------Cistus ladanifer type

2b Lumina all small < 4 μm----------3

3a Walls of the lumina > 2 μm thick and arranged into pole to pole striae. Columellae large > 2 μm and muri thick. ---------- Halimium type

3b Walls of the lumina not arranged in a striate pattern(if striae are present then they are short and run in all directions. Columellae < 2 μm, muri thin, lumina small < 2 μm----------Cistus salvifolius type

Tamaricaceae

Tamarix

Trizonocolpate reticulate grains, grain as long as broad, long colpi grain is small < 20 μm. Sculpturing is intectate-microreticulate, very similar to some of the small Cruciferae e.g. Capsella

Myrtaceae

Myrtus

Syncolpate grain, formed of three fused colpi, giving a triangular appearance, grain size is small < 15 μm and sculpturing is psilate.

Eucalyptus

Syncolpate grains, formed of three fused colpi, grain large >20 μm , angles of the grain thickened.

Umbelliferae

Bupleurum type

Trizonocolporate grains, as long as broad, and circular in polar view, columellae fine to indistinct. Pore protrudes.

Includes:- Berula

Hydrocotyle

As for Bupleurum but columellae are longest in the apocolpium giving a triangular appearance in polar view, columellae are coarse.

Echinophora.

Dizonocolporate grains, longer than broad with coarse columellae.

Ferula

Trizonocolporate grains, with the columellae longest at the poles, grain irregular in shape and is widest at the poles, costae present.

Elaeoselinum

As for Ferula but grain is regular and widest at the pores which do not protrude.

Eryngium

Trizonocolporate grains, costae absent and grains are large > 40 um, colpi short less than half the length of the grain and the rectangular pore protrudes.

Heracleum

As for Eryngium but colpi are long i.e. greater than half the length of the grain and the pores do not protrude.

Sanicula

Trizonocolporate grains, without costae and grain is < 40 µm in size and the pores do not protrude.

Pseudorlaya

As for Sanicula but the pores protrude, colpi are short.

Smyrnium

As for Pseudorlaya but colpi are long

Astrantia

Trizonocolporate grains, columellae are of an even thickness all over the grain. Grain large > 40 μm and the colpi are 90% the length of the grain, pores do not protrude.

Apium nodiflorum

Trizonocolporate grains, columellae are of an even length, grain < 40 μm and colpi are at least 90% length of the grain.

Crithmum type

As for Apium but colpi are only 60% length of the grain and costae are present, pore do not protrude.

Includes :- Carum which may be separable on a protruding pore.

Aethusa

As for Crithmum but costae are absent

Conopodium

Trizonocolporate grains with the columellae longest in the subequatorial region, costae present, pore does not protrude and grain is greater than 40 μm

Thapsia type

As for Conopodium but pore protrudes, grain is less than 40 μm and colpi are 60% length of the grain.

Includes :- Ligusticum, Peucedanum

Cachrys type

As for Conopodium but pore protrudes, grain < 40 μm and colpi are 60% length of the grain.

Includes:- Kundmannia, Magydaris, Aegopodium, Angelica

Pimpinella saxifraga type

Trizonocolporate grains, with the columellae longest sub-equatorially, costae are absent and pore does not protrude.

Psammogeton

As for Pimpinella but pore protrudes and columellae in the sub. eq. region are 3X as long as the rest of the columellae.

Myrrhis type

As for Psammogeton but columellae in the sub eq. region are less than 3x the rest of the columellae in the equator.

Includes:- Angelica and Torilis

Pastinaca

Columellae longest equatorially and extend into the sub eq. region. Costae absent and colpi are < 60% length of the grain and pore does not protrude.

Anthriscus type

As for Pastinaca but pore protrudes

Oenanthe

Trizonocolporate grains with the columellae longest in the equator, costae absent and pore protrudes.

Foeniculum type

Trizonocolporate grains, with the columellae longest equatorially , costae present and grain > 20 µm

Includes:- Apium graveolens, Caucaulis, Peucedanum

Conium type

As for Oenanthe but pore does not protrude

Includes :- Cicuta

Petroselinum

As for Foeniculum but grain < 20 µm

Key to the Umbelliferae

1a Grain as long as broad or nearly so----------2

1b Grain longer than broad----------3

2a Columellae of same length, grain circular in polar view, columellae fine-indistinct-----*Bupleurum* type

2b Columellae longest in the apocolpium, grain triangular in polar view, columellae coarse-----*Hydrocotyle*

3a Grain dizonocolporate----------*Echinophora*

3b Grain trizonocolporate----------4

4a Columellae longest at the poles----------5

4b Columellae longest down the sides or the same length-11

5a Costae absent----------7

5b Costae present----------6

6a Grain irregular in shape and widest at the poles ----------*Ferula*

6b Grain regular in shape and widest at the pores ----------*Elaeoselinum*

i) *Conopodium* may key out here but is large

ii) *Crithmum* may key out here but the pores protrude

7a Grain > 40 µm----------8

7b Grain < 40 µm----------9

8a Colpi < 50% length of the grain and pore protrudes ----------*Eryngium*

8b Colpi > 50% length of the grain and pore does not protrude----------*Heracleum*

i) *Smyrnium* may key out here but pore protrudes

9a Pore does not protrude----------*Sanicula*

9b Pore protrudes----------10

10a Colpi short----------*Pseudorlaya*

10b Colpi long----------*Smyrnium*

11a Columellae of the same length(some degraded specimens will key out this way)----------12

11b Columellae longest down the sides----------17

12a Grain > 40 µm----------13

12b Grain < 40 µm----------14

13a Colpi approx. 90% length of the grain, pore does not protrude----------*Astrantia*

(Some grains of *Conopodium* will key out here)

13b Colpi < 50% length of grain, pore protrudes--*Eryngium*

14a Colpi approx 90% length of grain-----*Apium nodiflorum*

14b Colpi approx 60% length of grain----------15

15a Costae present----------16

15b Costae absent----------*Aethusa*

16a Pore protrudes----------*Carum* type

16b Pore does not protrude----------*Crithmum* type

(Some grains of Conopodium will key out here but are large, also some grains of Aethusa and Aegopodium will also key out here).

17a Columellae longest subequatorially----------18

17b Columellae longest equatorially----------23

18a Costae present----------19

18b Costae absent----------21

19a Pore does not protrude, Grain> 40 µm----*Conopodium*

19b Pore protrudes, grain < 40 µm----------20

20a Colpi long, approx 80% length of grain--*Thapsia* type

20b Colpi short, approx 60% length of grain-*Cachrys* type

21a Pore does not protrude----------*Pimpinella saxifraga* type

21b Pore protrudes----------22

22a Columellae in the sub eq. region 3x longer than those at the equator----------*Psammogeton*

22b Columellae in the sub eq. region less than 3x longer then those at the equator----------*Myrrhis* type

Includes some grains of *Angelica* and *Torilis* but *Myrrhis* is longer

23a Costae present----------27

23b Costae absent----------24

24a Colpi < 60% length of grain----------25

24b Colpi > 80% length of grain----------26

25a Pore does not protrude----------*Pastinaca* type

25b Pore protrudes----------*Anthriscus* type

26a Pore protrudes----------*Oenanthe* type

26b Pore does not protrude----------*Conium* type

27a Grain < 20 μm ----------*Petroselinum*

27b Grain > 20 μm ----------*Foeniculum* type

Ericaceae

Calluna vulgaris

Tetrad irregular, coarsely verrucate and often with four colpi on each member of the tetrad.

Vaccinium vitis-idae

Tetrad regular, psilate to scabrate/verrucate sculpturing, with three colpi on each member of the tetrad. Colpi greater than half the length of the grain and costae colpi absent.

Erica umbellata

As for *Vaccinium* but costae colpi present and each member of the tetrad is joined for less than half the grain

E. tetralix type

As for *E. umbellata* but members of the tetrad join for more

than half the grain.

Includes:- E. cinerea, E. ciliaris, Vaccinium myrtillus

Arbutus type

As for E. tetralix but shape of the individual grains is not prominent in the tetrad giving a spheroidal appearance to the tetrad.

Erica australis type

As for E. tetralix but pore is not apparent and the colpus is narrow and crack like and tetrad diameter > 45 µm

Includes:- Arctostaphylos and Andromeda

Erica vagans type

Tetrad regular, costae colpi +, colpus narrow and crack like, edge of colpus well defined.

Includes:- Daboecia

Erica lusitanica type

As for E. vagans but colpu edge is diffuse.

Includes:- non porate members of E. tetralix, plus E.lusitanica E. scoparia, E. arborea, Phyllodoce, Loiseuleria, E. ciliaris.

Empetrum nigrum

Tetrad regular, colpi < half the length of the grain, tetrad < 30 µm

Rhododendron ponticum type

As for Empetrum but tetrad > 50 µm

Andromeda prolifera

As for Empetrum but tetrad diameter lies betwenn 40-50 µm, some other members of Rhododendron will also key out here

Corema album

As for Empetrum but tetrad diameter is 30-40 µm, costae colpi are prominent and tetrad gives a triangular shape due to

the poles of the individual grains being pointed.

Pyrola type

As for *Corema* but costae colpi ill-defined and tetrad is round.

Key to the Ericaceae

1a Tetrad irregular, coarsely verrucate, often with four colpi on each grain.----------*Calluna vulgaris*

1b Tetrad regular, psilate/scabrate/verrucate with three colpi on each member of the tetrad----------2

2a Colpi > 50% length ofthe grain----------3

2b Colpi < 50% length of the grain----------9

3a Costae colpi absent----------*Vaccinium vitis-idaea*

3b Costae colpi present----------4

4a Colpi wide and pore apparent----------5

4b Colpi narrow and pore not apparent----------6

5a Members of the tetrad join for less than 50% the length of the grain----------*Erica umbellata*

5b Members of the tetrad join > 50 % length of the grain.

----------*Erica tetralix* type

Arbutus will key out here but may be distinguished on shape

6a Members of the tetrad join for < 50% length of the grain----------*E. umbellata*

6b Members of the tetrad join > than 50% length of grain-7

7a Tetrad > 45 μm----------*E. australis* type

7b Tetrad < 45 μm----------8

8aEdge of colpus well defined---------*E. vagans* type

8b Edge of colpus diffuse----------*E. lusitanica* type

9a Tetrad < 30 μm----------*Empetrum nigrum*

9b Tetrad > 30 μm ----------10

10a Tetrad > 50 μm and pore sometimes apparent--
----------Rhododendron ponticum

10b Tetrad < 50 μm and pore never apparent----------11

11a Tetrad > 40 μm----------Andromeda

11b Tetrad < 40 μm----------12

12a Costae colpi prominent, tetrad triangular-Corema album

12b Costae colpi diffuse, tetrad round------Pyrola

Oleaceae

Phillyrea

Trizonocolporate grains, as long as broad, with a reticulum, muri thin and > 15 lumina across a mesocolpium.

Olea

Trizonocolporate reticulate grains, columellae large with the consequence that the muri are thick, < 12 lumin across the mesocolpium.

Fig 78 shows a frequency histogram of the number of lumina across a mesocolpium of :- 3 collections of P. angustifolia 2 collections of P. latifolia and 4 collections of Olea europaea

Boraginaceae

This key derives largely from the work of Clarke (1977) with additional material being incorporated from Spain.

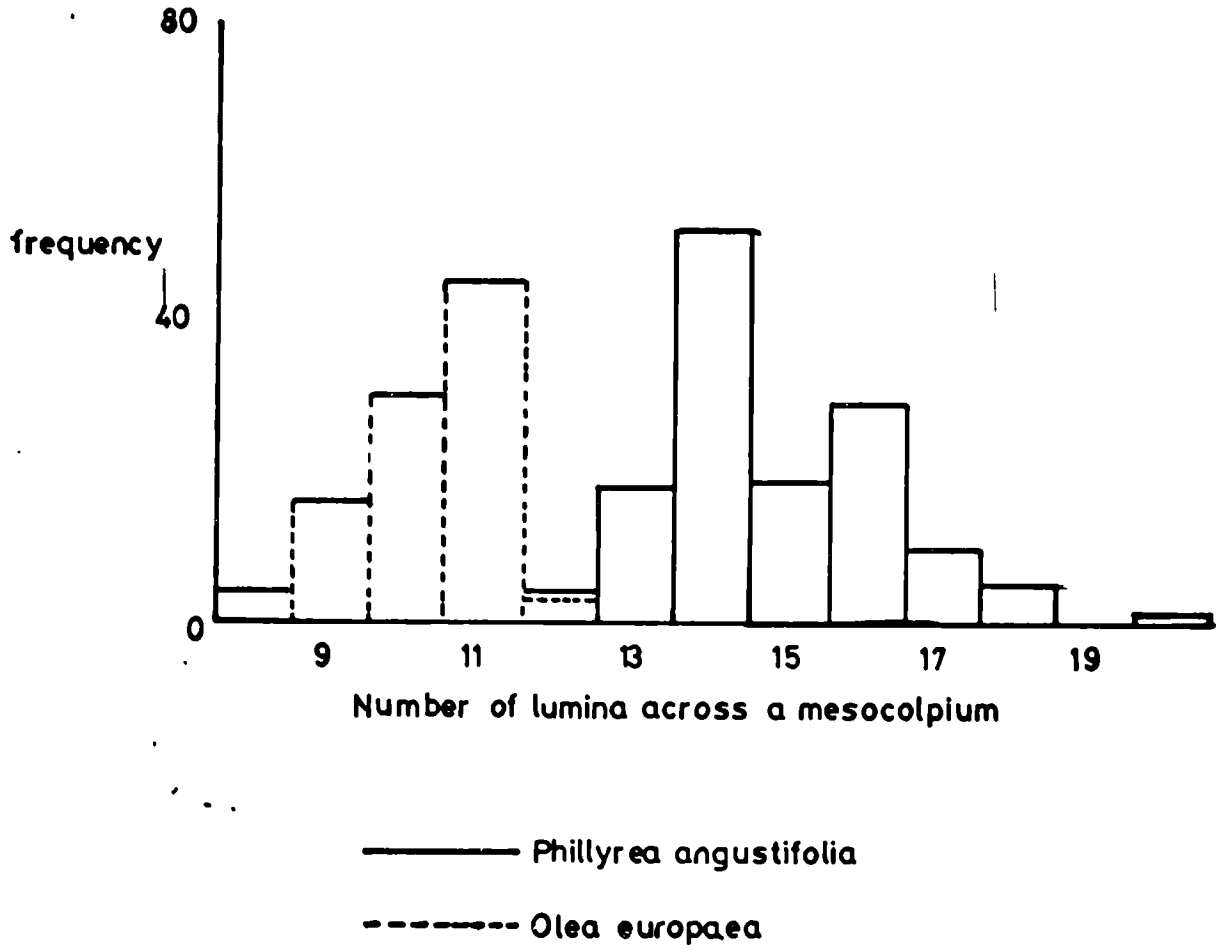
Echium

Trizonocolporate grains, microreticulate, grain 20-25 μm, pores are offset and one pole tends to be larger than the other giving a pear shaped appearance.

Alkanna type

Tr-tetrazonocolporate psilate grains, pores offset from the

Fig.78 Frequency histogram of number of lumina across a mesocolpium of Olea and Phillyrea



centre. Grain < 20 μm and one pole is larger than the other.

Includes :- Lithospermum

Onosmosa

Trizonocolporate grains, pori offset and one pole is larger than the other, sculpturing is granulate.

Anchusa arvensis

Tri-tetrazonocolporate, porus elongated equatorially, columellae distinct but exine is thin at the pole not like Borago. Sculpturing is granulate and grain > 40 μm.

Pentaglottis

Tri-tetrazonocolporate, endocolpi fuse to form a continuous endogirdle, grain microreticulate and > 20 μm

Pulmonaria

Trizonocolporate grains, columellae same length over grain and grain has reticulum developed only over the apertures.

Nonnea

Tetrazonocolporate with an endogirdle, grains reticulate at apertures only. Columellae shorter at the poles than at the equator.

Borago

8-9 colporate, columellae distinct and > 3 μm thick at poles. Sculpturing is granulate with an endogirdle present.

Symphytum

Octozonocolporate , but endocolpus does not fuse to form a continuousendogirdle, colpi are short, sculpturing scabrate.

Solenanthus

Hexazonocolporate grain, < 15 μm, continuousendogirdle present and grain convex at the equator.

Cerinthe major

Hexazonocolporate but ony three of the colpi carry pores (i.e.heterocolpate), nonporate colpi are shorter than the porate colpi. No endogirdle present and grain < 20 um and has psilate sculpturing.

Heliotropium

As for Cerinthe but porus is indistinct.

Cynoglossum

Like Heliotropium but grain < 20 μm

Lappula type

Like Heliotropium but grain < 20 μm and is constricted at the equator, pori are offset from the centre.

Omphalodes type

As for Lappula but pori are situated at the equator.

Includes Myosotis

Key to the Boraginaceae

1a All colpi with endoapertures----------2

1b Pollen heterocolpate----------12

2a Pollen having < = 5 colporate----------3

2b Pollen more than 5 colporate----------9

3a Pores offset from the centre and one pole larger than the other----------4

3b Pores in the centre and poles equal----------6

4a Grain microreticulate----------Echium

4b Grain psilate/granulate----------5

5a Grain psilate----------Alkanna type

5b Grain finely granulate----------Onosmosa

6a Grain reticulate even if just over the endoapertures, grain < 40 μm----------7

6b Grain psilate-granulate and > 40 μm------Anchusa arvensis

7a Grain with microreticulum over the whole grain (endogirdle present)----------Pentaglottis

7b Grain has reticulum developed only over the endoapertures-8

8a Columellae of even length----------Pulmonaria

8b Columellae longest in thesub eq.region---Nonnea

9a Grain 8 or 9 colporate----------10

9b Grain 6 colporate----------11

10a Columellae distinct(X1000) greater than 3 μm thick at the poles and an endogirdle present--------Borago

10b Columellae indistinct, exine thin over the poles, endocolpi do not unite to form an endogirdle-Symphytum

11a Endogirdle present, grain convex at equator-Solenanthus

11b No endogirdle and grain is concave at equator- Cerinthe

12a Grain ≥ 25 μm----------Heliotropium

12b Grain < 20 μm----------13

13a Grain constricted at the equator----------14

13b Grain not constricted----------Cynoglossum

14a Pori offset from equator----------Lappula

14b Por situated at the equator----------Omphalodes type

Labiatae

Teucrium

Trizonocolpate grain, sculpturing scabrate/verrucate , regularly spaced columellae present, tectum thick at apocolpium.

Lamiastrum galeobdolon

As for Teucrium but no thickening of the apocolpium and the scabrae are of varying sizes.

Marrubium

Trizonocolpate eureticulate , columellae distinct and duplicolumellate reticulum present.

Stachys alpina

Trizonocolpate microreticulate grains, colpi wide no costae, grains < 25 μm and columellae distinct.

Phlomis type

Trizonocolpate suprareticulate grains, lumina in middle of mesocolpium > 2.5 μm and the muri wind.

Includes :- Ajuga chamaepitys

Stachys palustris type

Trizonocolpate suprareticulate grains, lumina decrease to the colpus edge and are approximately 1 μm in the middle of the mesocolpium, muri wind, colpi wide and boat shaped, columellae distinct.

Includes :- S. erecta, Scutellaria minor, S. galericulata Galeopsis speciosa, Ballota nigra, Melittis and Prasium.

Stachys sylvatica type

Trizonocolpate suprareticulate grains, lumina of uniform size and less than 1 μm in middle of mesocolpium, columellae distinct.

Includes:- Lamium and Leonurus

Ajuga reptans

As for S. palustris but reticulum is not well developed in the apocolpium.

Sideritis

Tetrazonocolpate suprareticulate grains.

Prunella type

Hexazonocolpate suprareticulate grains.

Includes:- Hyssopus, Calamintha, Melissa, Cleonia, Nepeta, Glechoma.

Mentha type

Hexazonocolpate eureticulate grains, sometimes tec.-perf.

Includes:- *Salvia*, *Clinopodium*, *Origanum*, *Acinos*, *Micromeria*, *Satureja*, *Hormium*, *Ziziphora*, *Lavandula*, *Rosmarinus*, *Thymus*, *Lycopus*.

Key to the Labiatae

1a Trizonocolpate reticulate or scabrate/verrucate-------2

1b Hexazonocolpate grains or Tetrazonocolpate, grains reticulate never scabrate/verrucate.----------9

2a Sculpturing scabrate/verrucate----------3

2b Sculpturing reticulate----------4

3a Regularly spaced verrucae present, apocolpium visibly thickened----------*Teucrium*

3b Scabrae of varying sizes present and apocolpium not thickened----------*Lamiastrum galeobdolon*

4a Grain eureticulate and muri duplicolumellate--*Marrubium*

4b Grain suprareticulate and not duplicolumellate--------5

5a Grain < 20 µm, reticulum microreticulate--*Stachys alpina*

5b Grain > 20 µm, microreticulate or large lumina present-6

6a Reticulum in middle of mesocolpium > 2.5 µm wide, muri wind prominently----------*Phlomis* type

6b Reticulum < 2 µm in middle of mesocolpium, muri ± wind----------7

7a Lumina decrease to the colpus edge and lumina > lum in middle of mesocolpium---------*Stachys palustris* type 8

7b Lumina all same size and microreticulate-*Stachys sylvatica* type

8a Reticulum not developed in the apocolpium--Ajuga reptans

8b Reticulum developed in the apocolpium--Stachys sylvatica t.

9a Grain tetrazonocolpate----------Sideritis

9b Grain hexazonocolpate----------10

10a Grain suprareticulate, best developed in the middle of the mesocolpium on a bed of even columellae--Prunella type

10b Grain eureticulate- tec. perf., columellae sitting in a reticulate pattern under the muri------Mentha type

Solanaceae

Mandagora

Inaperturate grain with a trilete mark and echinate sculpturing.

Datura suaveolens

Inaperturate grain with large striae that wind longitudinally into the poles.

Datura stromarium

Trizonocolpate grains with short colpi, sculpturing is a eureticulum, muri wind

Physalis

Trizonocolpate grains with short colpi, sculpturing is large verrucae.

Solanum

Trizonocolporate grains, psilate, costae present, grain < 20 µm

Nicotiana

Trizonocolporate grains, scabrate/verrucate---reticulate/striate, costae present and grain > 20 µm.

Cestrum parqui

Trizonocolporate grains, > 40 µm, costae present, verrucate to striate and exine carries over in a lip over the colpus.

Key to the Solanaceae

1a Grain inaperturate or with a trilete mark----------2

1b Grain 3-4 colpate or 3 colporate----------3

2a Grain with a trilete mark and echinate---Mandragora

2b Grain possessing large striae winding longitudinally into the poles----------Datura suaveolens

3a Grain trizonocolpate----------4

3b Grain trizonocolporate----------5

4a Columellae sit in a reticulate pattern, colpi short, muri wind----------Datura stromarium

4b Sculpturing with large prominent verrucae---Physalis

5aGrain psilate and < 20 µm----------Solanum

5b Grain scabrate/verrucate-reticulate/striate, grain > 20 µm----------6

6a Grain scabrate/verrucate-reticulate/striate-Nicotiana

6b Grain verrucate----------7

7a Grain > 40µm, exine carries over colpus in a lip ----------Cestrum parqui

7b Grain < 40 µm ,no extension of exine----Withania type includes Lycopersicon

Scrophulariaceae

Pedicularis

Syncolpate consisting of two colpi, grain often split, psilate, columellae indistinct.

Mimulus

Syncolpate, colpus in a spiral, columellae distinct and sculpturing is reticulate.

Tozzia alpina

Trizonocolpate,reticulate, scabrae/verrucae underlie the

microreticulum, costae present, columellae distinct.

Melampyrum

Trizonocolpate, psilate-pilate sculpturing, columellae distinct, costae present.

Sibthorpia

Trizonocolpate, costae +, grain has bridge to the colpus, psilate sculpturing.

Rhinanthus type

Trizonocolpate grain, colpi thin and crack like, psilate sculpturing.

Includes:- Bartsia, Bellardia, Parentucella, Euphrasia Erinus, Veronica.

Gratiola

Trizonocolpate, psilate/verrucate, costae+, extension of the exine over the colpus is present, columellae fine-indistinct.

Scrophularia type

Trizonocolporate reticulate grains, columellae distinct, some lumina in the middle of the mesocolpium > 1 μm.

Includes:- Chanaerhinum, Asarina, Misopates, Verbascum

Digitalis

Trizonocolporate microreticulate, columellae distinct, grain > 20 μm and colpi > 7μm wide at the equator.

Linaria

As for Digitalis but < 20 μm and colpi narrow

Key to the Scrophulariaceae

1a Grain syncolpate----------2

1b Grain 3 or 4 colpate or colporate----------3

2a With two colpi fused at the poles, colpi ragged, grain often split, columellae fine-indistinct---Pedicularis

2b With one long spiral colpus, columellae distinct, grain reticulate----------*Mimulus*

3a Grain trizonocolpate----------4

3b Grain trizonocolporate----------8

4a Grain reticulate----------*Tozzia alpina*

4b Grain psilate-psilate/scabrate----------5

5a Exine thickest, columellae longest and more spaced out in the mesocolpium near the colpus and in apocolpium. Columellae short and densely packed in the middle of the mesocolpium and colpus edge---------*Melampyrum*

5b Columellae of equal length and distribution----------6

6a Grain with bridge to the colpus, costae large and prominent----------*Sibthorpia*

6b Grain with only a constriction of the colpus, costae absent----------*Rhinanthus* type

7a Grain psilate/verrucate and columellae fine to indistinct----------*Gratiola* type

7b Grains reticulate and columellae distinct----------8

8a At least some lumina in middle of the mesocolpium > 1 µm ----------*Scrophularia* type

8b All lumina < 1 µm----------9

9a Grain > 20 µm, colpi wide at equator----*Digitalis*

9b Grain < 20 µm, colpi narrow----------*Linaria* type

Includes:- *Anarhinum*, *Lindernia*, *Kickia*, *Cymbalaria* *Chaenorhinum*

Globulariaceae

Globularia repens

Trizonocolpate grains, spheroidal, microechinate.

Acanthaceae

Acanthus mollis

Trizonocolporate grains, longer than broad, columellae distinct and regularly spaced, around each columella exists a clear zone from which wall elements are absent.

Plantaginaceae

Plantago alpina

Polypantoporate, annulate, psilate to slightly verrucate grains 6-8 pores.

Plantago coronopus type

Polypantoporate(5-7), verrucate, pori annulate and microechinae cover the tectum and verrucae.

Includes P. serraria

Plantago lanceolata type

Polypantoporate grains (9-13), verrucate, pori annulate, microechinae cover the grain and verrucae.

Includes P. lagopus

Plantago albicans

Polypantoporate(7-9), pori not annulate, microechinae cover the verrucae and pore is distinct.

Plantago maritima type

Polypantoporate(6-7 rarely 8), no annulus, microechinae cover the verrucae.

Includes :-P. arenaria and P. afra

Plantago media

Polypantoporate(8-9) as for P. maritima

Plantago major type

Polypantoporate (5-7), pore indistinct, microechinae do not cover the verrucae. Annulus absent.

Plantago nivalis

As for P.major but often has 8 pores.

Littorella

Polypantoporate (10-11) , microechinae indistinct and grains > 30 µm.

Key to the Plantaginaceae

1a Annulus present----------2

1b Annulus absent----------4

2a Verrucae absent or indistinct----Plantago alpina

2b Verrucae present and prominent----------3

3a Pori < 7----------Plantago coronopus type

3b Pori > 7----------Plantago lanceolata type

4a Microechinae cover the verrucae----------5

4b Microechinae only occur between the verrucae----------8

5a Pore distinct but no annulus, approx. 8 pori
----------Plantago albicans

5b Pori diffuse, seen only by the interruption of the verrucate sculpturing----------6

6a Pori <= 7----------Plantago maritima type

6b Pori > 7----------Plantago media ------7

7a Grain > 30 µm, m.ech indistinct--Littorella

7b Grain < 30 µm, m.ech. distinct---Plantago media type

8a Pori approx 6----------Plantago major type

8b Pori approx 8----------Plantago nivalis

Dipsacaceae

Dipsacus type

Trizonoporate echinate, all spines equal approx. 2 µm, distinct annulus to pore, wall thick 5 µm.

Cephalaria

Trizonoporate echinate, dimorphic spines which sit on cushions on the tectum, large spines approx 2 μm, pore annulate.

Knautia arvensis

Trizonoporate echinate, dimorphic spines, annuli absent, large echinae approx 4 μm long.

Includes :- K. macedonia

Knautia dipsacifolia

Trizonocolpate echinate, costae absent, dimorphic spines.

Succisa

Trizonocolpate, echinate grains, circular in both the equatorial and polar view, columellae large 1-1.5 μm.

Scabiosa type

As for Succisa but grain is elliptic in equatorial view, columellae longest in apocolpium and < 1μ.

Includes:- Pterocephalus

Key to the Dipsacaceae

1a Grain trizonoporate echinate----------2

1b Grain trizonocolpate echinate----------4

2a Spines monomorphic approx 2 μm long-------Dipsacus

2b Spines dimorphic----------3

3a Annulus distinct, large spines sit on cushions and < 2 μm.----------Cephalaria syriaca

3b Annulus indistinct, large echinae > 3.5 μm-Knautia arvensis

4a No costae to colpus present--------Knautia dipsacifolia

4b Costae present----------5

5a Grain circular in polar and equatorial view, sexine of similar thickness, columellae large > 1.5 μm--Succisa

5b Grain circular in polar view but elliptic in equatorial view, sexine thick and columellae longest in the apocolpium, columellae < 1 µm--------*Scabiosa* type

Compositae

Liguliflorae

Fenestrate grains.

Includes:- *Taraxacum*, *Tragopogon*, *Arnoseris*, *Cichorium*, *Hypochaeris*, *Hieracium*, *Lapsana*, *Leontodon*, *Lactuca*, *Picris*, *Sonchus*, *Cicerbita*, *Prolonga*, *Phalocarpus*, *Scolymus*, *Catanache*, *Hispidella*, *Tolpis*, *Hyoseris*, *Urospermum*, *Chondrilla*, *Riechardia*, *Hedynopsis*.

Cousinia type

Trizonocolporate, psilate- scabrate/verrucate, no endocolpus, coarse columellae overlain by fine rods.

Centaurea cyanus

Trizonocolporate, scabrate/verrucate, continuous endogirdle present, with costae present along it.

Centaurea depressa type

Trizonocolporate, scabrate/verrucate, endogirdle incomplete and costae absent from it.

Includes:- *C. triumfetti*

Artemisia

Trizonocolporate echinate, echinae < 1.5 µm, tectum solid and columellae longest in the mesocolpium, porus never elongated.

Ambrosia type

Trizonocolporate echinate, echinae < 1.5 µm, tectum not solid, fine rods present, columellae distinct. Only fine rods of

tectun present. Grain < 35 μm and colpi are short < 1/3 the length of the grain.

Xanthium type

As for Ambrosia but columellae indistinct

Centaurea nigra type

Trizonocolporate echinate, endogirdle present, Grain > 35 μm Tectum not solid.

Includes :- C. iberica, C. juncea, C. nemoralis, C. pulchella, C. pullata, C. sphaerocephala.

Cnicus benedictus

As for C. nigra but the endogirdle is absent.

Centaurea scabiosa

Trizonocolporate echinate with all the echinae < 1.5 μm. Columellae visible under the fine rods of the tectum and a transverse endocolpus is present.

Jurinea type

As for C. scabiosa but no transverse endocolpus.

Anthemis type

Trizonocolporate echinate, spines > 1.5 μm, tectum underlain by coarse columellae.

Includes:- Achillaea, Chrysanthemum, Matricaria, Tripleurospermum, Santolina, Chamaeleum, Cladanthus, Soliva Anacyclus.

Aster type

As for Anthemis type but no coarse columellae present only fine rods of the tectum, echinae > 3μm.

Includes :- Petasites, Tussilago, Filago, Calendula

Bidens type

As for Aster type but echinae < 3μm and greater than 1.5 um.

Includes:- Inula, Pulicaria, Eupatorium, Erigeron, Bellis, Senecio, Gnaphalium, Solidago, Antennaria, Bellium, Crinitaria, Evax, Leontopodium, Carpesium, Asterias, Argotheca, Homogyne, Adenostyles, Arnica, Doronicum, Ligularia.

Cirsium type

Trizonocolporate echinate, echinae > 1.5 μ, grain > 35 μm, columellae visible under tectum, and are slanted under the echinae producing a star shaped pattern under LO analysis.

Echinops

As for Cirsium but grain > 60 μm and walls are thick > 10 μm the columellae are perpendicular under the echinae.

Serratula type

As for Cirsium but columellae are perpendicular under the echinae.

Includes:- Onopordon, Carduncellus, Mantisalca, Leuzea, Staehelina, Atractylis, Carlina, Xeranthemum, Sausserea and Arctium.

Carthamnus lanatus

Trizonocolporate echinate grains, echinae > 1.5 μm, grain > 35 μm, no coarse columellae present, colpi are short < 1/3 length of the grain.

Carduus type

As for C. lanatus but colpi are long.

Includes:- Silybum, Crupina, Tyriminus, Cynara, Notobasis, Ptilostemon, Galctites.

Key to the Compositae

1a Grain fenestrate----------Liguliflorae.

1b Grain trizonocolporate----------2

2a Grain psilate-scabrate/verrucate----------3

2b Grain echinate or echinate/verrucate----------5

3a Grain has a transverse endocolpus----------4

3b Endocolpus absent----------*Cousinia*

4a Endogirdle complete with costae------*Centaurea cyanus*

4b Endogirdle incomplete, costae- ------*Centaurea depressa* type

5a Protuberances < 1.5 μm high, all tiny echinae------6

5b Protuberances > 1.5 μm high----------12

6a Tectum solid, columellae distinct, and longest in the mesocolpium, porus never elongated---*Artemisia*

6b Tectum not solid, contains fine rods and columellae ± distinct----------7

7a Columellae not visible under the tectum, only the finely densely packed rods of tectum are visible----------8

7b Columellae visible, which are coarse and underlie the fine rods of the tectum----------10

8a Grain < 35 μm and colpi short----------*Ambrosia* type

8b Grain > 35 μm----------9

9a Grain with endogirdle and elliptic in equatorial view ----------*Centaurea nigra*

9b Grain without an endocolpus, circular in equatorial view ----------*Cnicus benedictus*

10a Grain with an endocolpus, exine thick at poles ----------*Centaurea scabiosa*

10b Grain without endocolpus, exine thickest at the equator----------11

11a Colpi short----------*Xanthium*

11b Colpi long----------12

12a Columellae branched, wall in equatorial region is 2x

as thick as that at the pole---------Cousinia

12b Columellae unbranched, large and irregular. No great variation in wall thickness----------Jurinea

13a Grain < 35 µm----------14

13b Grain > 35 µm----------16

14a Structured tectum underlain by coarse columellae ----------Anthemis type

14b Structured tectum not underlain by columellae, only fine rods of tectum visible----------15

15a Echinae > 3 µm----------Aster type

15b Echinae < 3µm----------Bidens type

16a Columellae visible under the tectum----------17

16b Columellae not visible under tectum----------19

17a Columellae slanting under the echinae, giving a star shaped pattern on LO analysis----------Cirsium

17b Columellae perpendicular under the echinae--------18

18a Grain> 60 µm, wall > 10 µ thick, grain triangular in polar view.----------Echinops

18b Grain < 60 µm, wall < 10 µm thick-------Serratula type

19a Echinae > 3 µm----------Aster type

19b Echinae < 3 µm----------20

20a Grain elliptic in equatorial view, endogirdle present ---------Centaurea nigra type

20b Grain circular in equatorial view, endogirdle absent.--21

21a Colpi short < 33% length of grain----Carthamnus lanatus

21b Colpi longer than 33% length of grain--Carduus type

Monocotyledons

Dipcadi serotinum

Inaperturate verrucate irregular grains.

Crocus

Inaperturate echinate grain, > 50 μm columellae indistinct.

Smilax aspera

Inaperturate echinate grain, < 35 μm and columellae fine-indistinct.

Colchicum type

Di-Tetra porate grains, pori irregular just ruptures in the tectum, grain reticulate with some of the lumina > 1 μm.

Includes Bulbocodium

Merendera type

As for Colchicum but lumina < 1 μm.

Borderea pyrenaica

Dizonocolpate, verrucate/scabrate, columellae club shaped to polyhedral in shape.

Chamaerops humilis

Dicolpate grain with both colpi on one side of the grain, sculpturing is microreticulum.

Tamus

Dizonocolpate grains, reticulate, columellae visible and lumina get smaller to the colpus edge.

Tofeldia

Dizonocolpate reticulate grains with lumina of same size. Columellae invisible and grain < 25 μm , exine thin

Dracaena

Monocolpate, psilate-scabrate, columellae fine-indistinct, grain < 40 μ

Muscari type

Monocolpate, heterbrochate reticulum, grain < 40 μm

Includes Aphyllanthes.

Phoenix type

Monocolpate grain, tectate perforate, columellae distinct, Grain < 40 µm

Includes Asparagus

Narthecium

Monocolpate reticulate grains, columellae indistinct and reticulum never heterobrochate.

Veratrum type

As Narthecium but reticulum gets smaller to the colpus edge and the columellae are distinct.

Includes Butomus

Convallaria type

Monocolpate tectate perforate grains, grain > 40 µm

Includes:- Narcissus, Mainthemum, Polygonatum, Paris, Gagea

Allium type

Monocolpate tectate perforate- scabrate/verrucate grains, columellae indistinct.

Includes:- Leucojum, Galanthus

Asphodelus

Monocolpate, tectate perforate-scabrate/verrucate grains, which are as long as broad, grain > 75 µm, colpi wider in the middle.

Gladiolus type

As for Asphodelus but grain is < 40 µm and scabrae are coarse and uneven.

Yucca

As for Gladiolus but scabrae are even and formed by the columellae.

Lapiedra

Monocolpate, microreticulate grain which is > 40 µm.

Iris type

Monocolpate reticulate grain, lumina > 1µ and muri duplicolumellate.

Includes Sternbergia

Lilium

Monocolpate reticulate heterobrochate grains which are > 90 µm

Bellevallia

Monocolpate reticulate heterobrochate grains < 90 µm, lumina larger in centre of grain and colpus is long > 50% length of grain.

Scilla type

As for Bellevallia but colpus is short and large lumina distributed evenly over the whole grain.

Includes:- Hyacinthus, Pancratium, Frittilaria, Urginea Erythronium, Hyacinthoides and Eremurus.

Key to the Monocotyledons

1a Grain inaperturate----------2

1b Grain has colpi or pores----------4

2a Grain verrucate and irregular in shape-----Dipcadi serotinum

2b Grain echinate----------3

3a Grain > 50 µm, columellae visible-------Crocus

3b Grain < 35 µm and columellae fine-indistinct-Smilax aspera

4a Grain has pores or irregular ruptures----------5

4b Grain is colpate----------6

5a Lumina > 1µm----------Colchicum type

5b Lumina < 1µm i.e. microreticulate-------Merendera type

6a Grain dizonocolpate----------7

6b Grain monocolpate----------10

7a Scabrae/verrucae present or columellae club shaped or in polyhedral shapes----------*Borderea pyrenaica*

7b Reticulate sculpturing present, never s/v----------8

8a Both colpi on one side of grain---*Chamaerops humilis*

8b Colpi arranged dizonocolpate----------9

9a Columellae visible, lumina get smaller to the colpus--*Tamus*

9b Columellae invisible, lumina constant, exine thin < 1μm, grain < 25 μm----------*Tofeldia*

10a Grain < 40 μm----------11

10b Grain > 40 μm----------15

11a Sculpturing tectate perforate or scabrate/verrucate--12

11b Sculpturing reticulate----------13

12a Grain psilate-scabrate/verrucate, columellae indistinct ----------*Dracaena*

12b Grain tectate perforate, columellae distinct--*Phoenix* type

13a Reticulum is heterobrochate----------*Muscari* type

13b Reticulum never heterobrochate----------14

14a Lumina of constant size, columellae indistinct ----------*Narthecium*

14b Lumina decrease to colpus edge,columellae distinct. ----------*Veratrum* type

15a Grain tectate perforate/psilate/scabrate/verrucate--16

15b Grain reticulate----------20

16a Grain tectate perforate----------*Convallaria* type

16b Grain scabrate/verrucate-psilate----------18

17a Grain psilate, with some faint verrucae, columellae indistinct----------*Allium* type

17b Grain scabrate/verrucate, columellae distinct-----18

18a Grain elongate, colpi wide all the way along its length, tendency to irregular scabrae, or if regular never round, grain < 70 μm----------19

18b Grain as long as broad, colpus widens for half its length, grain > 75 μm----------*Asphodelus*

19a Scabrae formed by the columellae coarse and uneven ----------*Gladiolus*

19b Scabrae of a regular shape----------*Yucca*

20a Grain heterobrochate and muri duplicolumellate---- *Iris* type

20b Lumina of a constant size and the wall supported by only one row of columellae---------- 21

21a Grain > 90 μm----------*Lilium*

21b Grain < 90 μm----------22

22a Grain with lumina in centre larger than at the colpus edge, colpi long > 50% length of grain---*Bellevallia*

22b Grain with large lumina distributed evenly over the tectum, colpi long----------*Scilla* type

APPENDIX B

Pollen Extraction

Procedure

Pollen Extraction Procedure

1. Approximately $1cm^3$ of the sample was removed from the required level, after cleaning the surface of the core. All samples were then placed in a boiling tube and 10 ml of KOH (10%) added, which was then placed in a boiling water bath for ten minutes. (Distilled water was added at intervals to prevent the KOH becoming too concentrated.

2. The samples were then sieved through a 100 μm aperture sieve into a plastic centrifuge tube. The washings were made up with distilled water and then centrifuged at 3000 r.p.m. for 3 minutes.

3. The liquid was decanted and 6 ml of 40% HF added. The samples were then placed in a boiling water bath for various periods of time, dependent on the siliciousness of the samples (See text for actual times).

4. Samples were then centrifuged as before and the liquid decanted into a suspension of $Ca(OH)_2$ in dilute KOH to neutralize the HF. (In a Fume Cupboard).

5. The pellet was resuspended in 10% HCl, to dissolve any residual silico-fluorides. Tubes were warmed and then centrifuged and decanted as before.

6. The pellet was resuspended in glacial acetic acid in order to dehydrate the sample prior to acetolysis. The samples were then centrifuged and decanted as before.

7. Ertdman (1960) acetolysis procedure was then performed by adding 6 ml of acetolysis mixture (9:1 acetic anhydride: conc H_2SO_4) to the tubes which were then placed in a boiling water bath for 3 minutes and then centrifuged and decanted into running water.

8. Pellet was resuspended in glacial acetic acid, centrifuged and decanted.

9. The pellet was then resuspended in distilled water with a few drops of KOH added to neutralize the acid and render the pollen more susceptible to safranin staining. Centrifuged and decanted.

10. Four drops of aqueous safranin were added and then 2 ml of distilled water. Centrifuged and decanted.

11. Pellet was resuspended in 1.5 ml of glycerol jelly and mixed thoroughly, slides were prepared from this mixture.